Foraging in Plants: the Role of Morphological Plasticity in Resource Acquisition

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> Triffids were, admittedly, a bit weird—but that was, after all, just because they were novelties. People had felt the same about novelties of other days—about kangaroos, giant lizards, black swans. And, when you came to think of it, were triffids all that much queerer than mudfish, ostriches, tadpoles, and a hundred other things? The bat was an animal that had learned to fly: well, here was a plant that had learned to walk—what of that?
>
> (from John Wyndham, *The Day of the Triffids*, 1951)

I. SUMMARY

Resources which are essential for plant growth are usually heterogeneously distributed both in space and in time within the habitat. As a result of plasticity in the modular construction of branches ("spacers") in response to resource availability, plants are capable of placing leaves and root tips ("resource-acquiring structures") non-randomly within their environment. Selective placement of organs of resource uptake actively modifies the potential for resource acquisition, and is interpreted as a consequence of foraging behaviour.

There is ample evidence that plants are capable of placing resource-acquiring structures selectively within the habitat. Orthotropic (vertical) shoots commonly reduce spacer length and increase lateral branch formation under more favourable light conditions. These morphological modifications promote more effective placement of leaves in the high light zone at the top of a vegetation canopy. In many species increased lateral root formation and growth increases local root surface area in patches with high nutrient content. The morphological responses to resource supply from the environment are usually purely responses to local patch quality, and they are normally unaffected by the conditions experienced by other parts of the plant. In contrast to orthotropic stems, plagiotropic (horizontal) stems of clonal plants exhibit a variety of responses to resource availability, and the magnitude of response is usually much smaller than that seen in orthotropic shoots. Rather than providing the plant with a capacity to place ramets selectively in favourable patches within a heterogeneous environment, plagiotropic stems appear to be important for the continuous exploration of new habitat space.

Foraging behaviour which enhances the probability of locating resource-rich patches does not appear to be profitable in all environments. In habitats

of inherently low resource availability, in which resources become available in the form of ephemeral pulses, physiological plasticity has been viewed as a profitable adjunct to morphological plasticity for the acquisition of resources. It has been proposed that morphological plasticity will be more restricted in plants which are characteristic of such conditions. Evidence is accumulating that shoots of shade-tolerant species are indeed morphologically less plastic than shoots of shade-intolerant species. However, it has not been conclusively shown that the root morphology of species from infertile soils is less plastic than that of species from fertile soils.

Physiological studies have demonstrated that the photosynthetic apparatus has the ability to utilize ephemeral sunflecks efficiently, and that plasticity in nutrient uptake rates promotes efficient capture of nutrient pulses. Few comparative studies have been carried out to date, but the available data show only a weak tendency for greater physiological plasticity in species from habitats with low light or low nutrient availability. In resource-poor habitats, the ability of resource-acquiring structures to remain viable during periods of resource depletion seems to be at least as important for the acquisition of resource pulses as a high level of physiological plasticity. In general, the relative importance of morphological *versus* physiological plasticity for resource acquisition in heterogeneous environments has yet to be assessed. We conclude that, to date, support is as yet incomplete for the contention that species from habitats which differ in resource supply possess different resource acquiring syndromes.

The ultimate aim of research into foraging should be to understand the benefits and disadvantages of different resource-acquiring syndromes, and their ecological and evolutionary consequences. Achievement of this goal requires evaluation of foraging behaviour in terms of its costs and benefits. There is also a need for an increase in information on the developmental and physiological traits—and the genetics of the traits—which underlie plasticity.

II. INTRODUCTION

All plant species require the same limited number of essential resources from their environment, namely sunlight, carbon dioxide, water and a number of elements in nutrient form, obtained, at least in higher plants, predominantly from the soil. The availability of these resources from the environment is patchy both in space and time. Therefore, the difficulty in obtaining sufficient resources varies spatially and temporally. Although there are differences between species in the levels of resources which are needed for growth, and although the ratios in which resources are required may differ between species, all plants have the same basic problems of resource acquisition to solve. This review is a discussion of the solutions employed by plants for enhancing the acquisition of essential resources in spatially and temporally heterogeneous habitats.

The possession of morphological plasticity and the ability to produce branched structures by the proliferation of modules are attributes which free plants from some of the limitations imposed by sessility. Resource-acquiring structures (these have also been referred to as "feeding sites" (Bell, 1984) and "mouths" (Watson, 1984)) such as leaves, root tips and, in clonal plants, ramets, are projected into the environment upon branches ("spacers"; Bell, 1984). When the part of the spacer proximal to a resource-acquiring structure stops extending, the position of that resource-acquiring structure becomes fixed. Evidence will be presented showing that many plants do not place their resource-acquiring structures in random positions within their environment, but instead place them selectively in patches of greater resource supply. Such morphological responses to resource availability may actively modify the potential of the plant for resource acquisition and they are interpreted as manifestations of foraging behaviour.

In the following section of this review we define and delimit the issues which will be discussed. In Sections IV–VI we document the foraging activities of the spacers and resource-acquiring organs of higher plants, and the foraging activities of fungi. These sections also review what is known about the proximal physiological and developmental mechanisms which control foraging activities. In Section VII we discuss integration—the extent to which foraging behaviour is coordinated throughout the whole plant. Physiological plasticity in the rates of resource acquisition by leaves and roots has been viewed as a profitable adjunct to foraging, and this topic is discussed in Section VIII. In the penultimate section (IX), we summarize the hypotheses which have been presented in the literature on foraging syndromes as adaptive traits in given environmental settings. These hypotheses are then evaluated, given the empirical evidence presented earlier. This section culminates in the formulation of a number of questions which remain to be solved. We conclude the review (Section X) by briefly outlining an agenda for a research programme on plant foraging, which includes proposals for empirical and mathematical studies on the costs and benefits of foraging behaviour.

III. DEFINING THE SCOPE OF THE REVIEW: ON FORAGING, PLASTICITY AND GROWTH

Description of plant responses to environmental quality in terms of foraging is a relatively recent development. To our knowledge, Bray (1954) was the first to use the term in this way when he described the search patterns of roots for nutrients in the soil. Later on, Grime and his co-workers (e.g. Grime, 1979; Grime *et al.*, 1986) established common usage of the term in the vocabulary of plant ecology. Here we define foraging as "the processes whereby an organism searches, or ramifies within its habitat, which enhance its acquisition of essential resources" (modified after Slade and Hutchings, 1987a). We believe that this definition fits the subject as it is perceived by animal ecologists and behaviourists. Foraging in plants is accomplished by morphological plasticity. As such it is one aspect of plant "behaviour", a term which has been widely used by plant ecologists in recent years as an alternative to phenotypic plasticity (Silvertown and Gordon, 1989).

Bradshaw (1965) has defined plasticity thus: "Plasticity is shown by a genotype when its expression is able to be altered by environmental influences. The change that occurs can be termed the response. Since all changes in the characters of an organism which are not genetic are environmental, plasticity is applicable to all intragenotypic variability." In response to different environmental conditions, morphological plasticity can generate different patterns of spacer production and hence different patterns in the placement of resource-acquiring structures. This review concentrates on analysis and interpretation of these patterns and their consequences for future resource acquisition.

Our definition emphasizes that placement of resource-acquiring structures is an essential component of foraging. It must be realized that under certain conditions a lack of selective placement may be an important element of a foraging syndrome; habitat heterogeneity may be such that selective placement will not contribute to an increase in resource acquisition. It is probable that in many cases plants use a combination of morphological and physiological techniques to acquire resources efficiently, with the balance of importance between these techniques depending on the type of habitat occupied. In analogy with animal foraging theory we postulate that the economics (i.e. the costs and benefits) of different resource-acquiring behaviours are reflected in the performance of the plant, and that in a given environmental setting the behaviour conferring the highest long-term resource gain will have a selective advantage.

In addition to plasticity in spacer morphology, plasticity in a number of other plant characteristics, such as root:shoot ratio, leaf and root turnover rates, and storage capability, will also influence resource acquisition or resource retention. Although the consequences of such variation can be investigated using economic principles (Bloom *et al.*, 1985; Chapin *et al.*, 1990) we do not regard variation in these characteristics as aspects of foraging behaviour, because the positioning of plant parts is not involved. They are thus largely omitted from this discussion.

Foraging is thus concerned with the placement of resource-acquiring structures within the surroundings of the plant, and its implications for future resource acquisition. Growth, by contrast, refers to the consequences of resource acquisition for the production of new modules or ramets and the concomitant increase in plant size. The distinction between growth and foraging must be clear. Consider two environments, one providing few resources and thus affording only slow growth, the other providing ample resources and supporting rapid growth. After a given length of time, two plants with identical genotypes will have achieved different biomasses in the two environments. If this is all that distinguishes them and if, in the course of time, the plant in poor conditions would come to resemble the plant in good conditions in both biomass *and* morphology, there would be no evidence that they have responded to the different conditions by foraging in different ways. They only differ in the extent to which they have grown. If the plants have responded to their environments by foraging, however, they will differ from each other in the morphology of their spacers and in the patterns of placement of their resource-acquiring structures. For example, plants of *Abutilon theophrasti* grown under high and low light conditions had very different shoot heights when compared at the same plant weight (Rice and Bazzaz, 1989). This is an indication that shoots foraged in these environments in different ways.

In analogy with the literature on foraging in animals, Kelly (1990) has suggested that responses in plants should only be accepted as foraging activities if they have taken place *prior to* resource uptake (see also Oborny, 1991). We regard such a limitation in the use of the concept as unnecessarily restrictive and difficult to apply because, unlike the situation in animals, resource uptake in plants is usually a continuous process. Moreover, resource uptake is often the only means by which a plant can sense the level of resource supply from its environment (the use of light *quality* detection is a notable exception, as will be discussed below). Rather than emphasizing the timing of foraging responses relative to the timing of resource uptake, we focus on the importance for future resource acquisition by the plant, of the ability to produce changes in its modular construction in different environments.

IV. THE FORAGING ACTIVITIES OF SHOOTS

Shoots do not all grow towards the strongest source of light. Those which do are usually referred to as orthotropic, although strictly they should be described as positively orthophototropic. However, many species produce stem homologues, such as stolons and subterranean rhizomes, which are oriented at some angle, rather than vertically (plagiotropically) or strictly horizontally (diagravitropically; see Salisbury and Marinos, 1985). In this section we review morphological plasticity in stems and their homologues. We discuss the effects of variation in a number of environmental factors on shoot morphology. This discussion is followed by a consideration of the proximal mechanisms regulating morphological plasticity. We conclude with an examination of the extent to which shoots will be capable of selective placement in the more favourable parts of a patchy environment as a consequence of the morphological responses which have been discussed.

A. Response to Photon Flux Density

The shoots of higher plants are constructed from a number of repeated building blocks or metamers (White, 1979). A metamer consists of a node, an internode, an axillary meristem and a leaf. The components of metamers may not all be equally conspicuous. For example, the leaf may be rudimentary, and may drop soon after the metamer is formed, or the internode may be compressed. Metamers are usually arranged in a monopodial axis, or module. Each module is terminated by an apex, which may be living, dead, vegetative or sexual. Axillary (or lateral) meristems may grow out and form new modules, but in many plants they remain dormant for long periods.

The most consistent plastic responses to availability of light are internode elongation (etiolation) and reduced branching (a lower proportion of axillary meristems grow out) at lower flux densities (e.g. Bazzaz and Harper, 1977; Ford and Diggle, 1981; Givnish, 1982, 1986; Smith, 1983; Jones, 1985; Maillette, 1985, 1986; Ellison, 1987; Menges, 1987; Ellison and Niklas, 1988). The etiolation response commonly takes place without a corresponding increase in shoot weight, and thus involves a change in shoot allometry, with etiolated internodes having lower weight per unit length (e.g. Ogden, 1970; Hutchings, 1986; Foggo, 1989; Rice and Bazzaz, 1989). The tendency to increase in height by etiolation varies between species with orthotropic shoots (Grime, 1966; Hara *et al.*, 1991), being more pronounced in shade-intolerant than in shade-tolerant species. Although increased height may promote overtopping of neighbours and improve access to light in some communities, it will not enable herbaceous species, or species of low stature, to avoid shade in woodlands (Fitter and Ashmore, 1974; Frankland and Letendre, 1978).

Height extension in response to low light availability has also been observed in some graminoids which lack a true orthotropic stem. For example, in *Carex flacca* (Cyperaceae) and *Brachypodium pinnatum* (Poaceae), shading stimulates leaf elongation and leaf sheath elongation respectively (de Kroon and Knops, 1990). When vegetation is dense, these responses could lift leaf blades into the high light zone of the canopy, enabling both more efficient photosynthesis and greater shading of neighbours. Increase in leaf sheath length can be protracted in time in *B. pinnatum*, with the degree of elongation depending on the local light regime, allowing a fine-scaled, efficient response to local canopy conditions. *B. pinnatum* and *C. flacca* also form plagiotropic rhizomes, the mean length of which does not change in *B. pinnatum* and decreases in *C. flacca* under low photon flux density, although the variations in rhizome lengths are large for both species under all growing

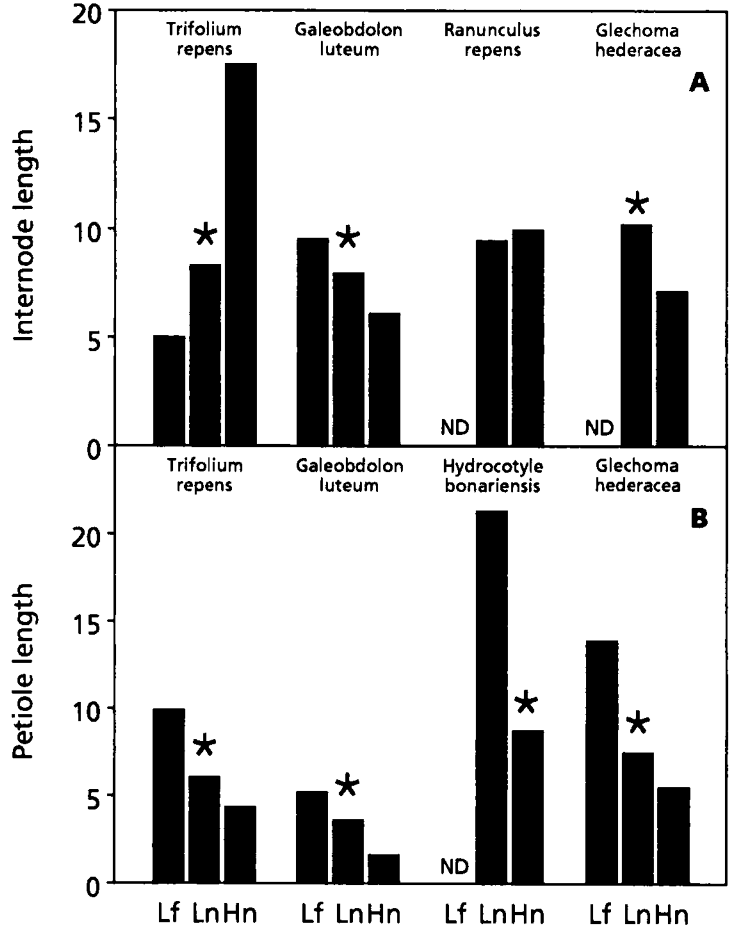

Fig. 1. Responses of (A) stolon internode length and (B) petiole length of some herbaceous stoloniferous species to photon flux density (PFD) and light quality. Treatments are: Lf, low photon flux density, filtered (low R/FR ratio); Ln, low photon flux density, neutral (high R/FR ratio); Hn, high photon flux density, neutral. *Trifolium repens* data from Thompson and Harper (1988): PAR under low photon flux density was 32% of PAR under high photon flux density; R/FR ratios in neutral and filtered light were approximately 1·0 and 0·2, respectively. Filtered light was produced by shade from a *Holcus lanatus* canopy. *Galeobdolon luteum* data from Mitchell and Woodward (1988): PAR under low photon flux density was 12% of PAR under high photon flux density; R/FR ratios in neutral and filtered light were approximately 0·85 and 0·40, respectively. *Ranunculus repens* internode data from Lovett Doust (1987): PAR under low photon flux density was 66% of PAR under high photon flux density. The results shown here are for plants of *R. repens* from a woodland population growing under high nutrient availability. *Hydrocotyle bonariensis* petiole data from Evans (1992): PAR under low photon flux density was 25% of PAR under high photon flux density. Results for severed plants growing under high nutrient and high water availability.

conditions. As in *C. flacca*, the main vertical shoots of *Glaux maritima*, a member of the Primulaceae, showed clear etiolation responses to low light, producing longer internodes, although the horizontal subterranean offshoots which produce hibernacles at their ends were shorter (Jerling, 1988).

Several species with plagiotropic stems etiolate under low light availability (Hutchings and Turkington, 1993), while others do not show a significant response (Fig. 1). In *Glechoma hederacea*, a shade-tolerant stoloniferous species, internode and petiole lengths increase and branching is reduced when photon flux density is low (Slade and Hutchings, 1987b; E.A.C. Price and M.J. Hutchings, 1993, unpublished). However, the total length of primary stolons hardly responds to light level (Hutchings and Slade, 1988). This is also true in *Ranunculus repens*, although in this species the lengths of individual internodes are unresponsive to light level (Lovett Doust, 1987). There is a fall in weight per unit length of stolon in both *G. hederacea* and *R. repens* when photon flux density is reduced. A species which is closely related to *G. hederacea, Lamiastrum galeobdolon* (syn. *Galeobdolon luteum*), also has longer stolon internodes and petioles under lower light levels (Mitchell and Woodward, 1988; Dong, 1993), as does *Hydrocotyle bonariensis* (Evans, 1992). In *Trifolium repens*, internode lengths are unresponsive or even shorter at low light levels, while stolon branching declines dramatically and vertical petioles etiolate as light supply declines (Solangaarachchi and Harper, 1987; Thompson and Harper, 1988). Thompson (1993) recently showed that the responses of *T. repens* depend on the actual photon flux densities that are applied. At relatively low light, an increase in flux density may result in an increase in stolon internode and petiole length but at higher light supply an increase in flux density may result in shorter structures.

Tropical vines use the support of host trees to reach high light zones in the top of the forest canopy. Vines employ a number of solutions to reach a suitable support. Slender leafless shoots of *Monstera gigantea* seedlings have been shown to grow preferentially towards "the darkest sector of the horizon", thus increasing the probability of encountering a nearby tree trunk up

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Fig. 1. (continued)
Glechoma hederacea internode data from Slade and Hutchings (1987b): PAR under low photon flux density was 25% of PAR under high photon flux density. Data for primary stolons only. *Glechoma hederacea* petiole data from E.A.C. Price and M.J. Hutchings (1993, unpublished): in the Ln treatment, PAR was 20% of PAR under high photon flux density and R/FR ratio was 0·9; in the Lf treatment PAR was 2·5% of PAR under high photon flux density and R/FR ratio was 0·45. Shading was imposed by competition with *Lolium perenne*. Data for primary stolons only. All mean lengths in cm except for *Trifolium repens* internodes, which are given in mm. Asterisks indicate significant differences between treatments at least at $p < 0{\cdot}05$. ND is not determined.

which the vine can grow (Strong and Ray, 1975). In deep shade, the tropical liana *Ipomoea phillomega*, and many other vine species (Ray, 1992) produce flagellar shoots with long internodes, high elongation rates and rudimentary, short-lived leaves (Peñalosa, 1983). Such shoots typically circumnutate, sweeping the terminal part of the shoot through the air as the result of an endogenous growth-related rhythm (Putz and Holbrook, 1991). Perception of nearby support can modify the rotational movement into an ellipse with the long axis oriented towards the support (Tronchet, 1977, cited in Putz and Holbrook, 1991). Circumnutation thus improves the chances of finding a suitable support. Once shoots have reached a support and commenced orthotropic growth, the slender stems may alter their form to produce shorter internodes. They also show slow elongation and eventually, upon reaching a zone of high photon flux density, develop large, long-lived leaves (Peñalosa, 1983; Ray, 1992). Similar morphological responses to open and shaded habitats are shown by the scrambling stem internodes of *Rubia peregrina* (Navas and Garnier, 1990).

B. Response to Light Quality

In terms of illumination, the habitats of most plants are patchy, consisting of areas where leaves can be illuminated by direct or diffuse sunlight, and areas where the light they receive first passes through the leaves of overhanging competing species. Light transmitted through leaves has a lower ratio of red/far-red (R/FR) light than unfiltered light (Holmes and Smith, 1975; Holmes, 1976, 1981; Hutchings, 1976). The R/FR ratio may fall from approximately 1·15 in full sunlight to as little as 0·05 under a dense canopy of vegetation. When plants are exposed to a R/FR ratio lower than that found in unfiltered light, stems develop a greater degree of apical dominance. This is expressed as an increase in stem elongation rate and an inhibition of the growth of lateral buds. Responsiveness differs between species (Grime, 1966, 1979; Child *et al.*, 1981; Morgan, 1981), with shade-tolerant species responding less than shade-intolerant ones (Morgan and Smith, 1979; Smith, 1982; Corré, 1983; Holmes, 1983). Light which has passed through plant leaves also has a lower proportion of blue light than is found in unfiltered light. Supplementing the blue light incident on a plant has been shown to induce the production of shorter internodes (Thomas, 1981; Quail, 1983; Schafer and Haupt, 1983). Thus, plants may be expected to produce longer internodes when beneath a canopy transmitting a low level of blue light.

Both in species with orthotropic and plagiotropic shoots, the largest effects of light quality on stem elongation are seen below the leaves of plants transmitting the lowest R/FR ratio (Smith and Holmes, 1977; Thompson and Harper, 1988). Although much of the information collected on these effects is for dicotyledonous species, similar effects are seen in grasses (Deregibus *et* *al.*, 1983; Casal *et al.*, 1985, 1987; Skálová and Krahulec, 1992). Supplementation of FR light stimulates shoot length elongation in grasses, with the response being most marked in the leaf sheaths. At the same time tillering is suppressed. That these changes can be induced by alterations to the light environment caused by plant density is shown by ingenious work by Deregibus *et al.* (1985) and Casal *et al.* (1985), in which red-light-emitting diodes were placed at the bases of plants of the grass species *Sporobolus indicus* and *Paspalum dilatatum*, increasing the R/FR ratio. Plants treated in this way produced more tillers than control plants grown at the same density (Fig. 2), thus aggravating local competition for light. It has been suggested that the greater apical dominance induced in control plants when density is high (and therefore R/FR ratio low) could promote escape from competitive situations if the energy saved on tillering was instead allocated to more or longer rhizomes.

Several recent studies (Ballaré *et al.*, 1987, 1988, 1990, 1991a; Casal *et al.*, 1990) have demonstrated that an increase in internode length can be caused by changes in the quality of the light reflected from the stems and foliage of neighbouring plants. As with light which has passed through a canopy of leaves, this reflected light has a low R/FR ratio. Changes in stem morphology can be induced by this reflected light well before the presence of the neighbouring plants causes measurable shading. This observation has led to the hypothesis that the change in the quality of light reflected from neighbouring plants may serve as an early warning of impending competition for light, allowing the plant to develop an appropriate morphological response before competition for light becomes intense. Similarly, *Portulaca oleracea*, a prostrate species with many scrambling stems which develop from a single rooted origin, grows preferentially away from shade and areas with high FR levels when placed in a heterogeneous light environment (Novoplansky *et al.*, 1990a). That light quality is more important as a signal than light quantity, is shown by the observation that seedlings of *P. oleracea* became recumbent preferentially in the direction of light with a higher R/FR ratio, rather than higher photon flux density (Novoplansky, 1991). A strong tendency to grow away from sectors of the horizon with a low R/FR ratio may also underlie observations by Strong and Ray (1975) showing that a tropical vine on the forest floor grows preferentially towards darkness rather than towards lighter sectors of its horizon that presumably have a low R/FR ratio.

We conclude this section with an exception to the general response of etiolation to low light levels and low R/FR ratios. The extreme densities which can be developed in pure stands of bryophytes produce very low light fluxes close to the surface of a moss turf (During, 1990). Severe stem etiolation might be expected in such colonies, accompanied by substantial shoot mortality, but many mosses do *not* etiolate when given light with a low R/FR ratio, and their mortality rates are low (Bates, 1988). There seems to be a

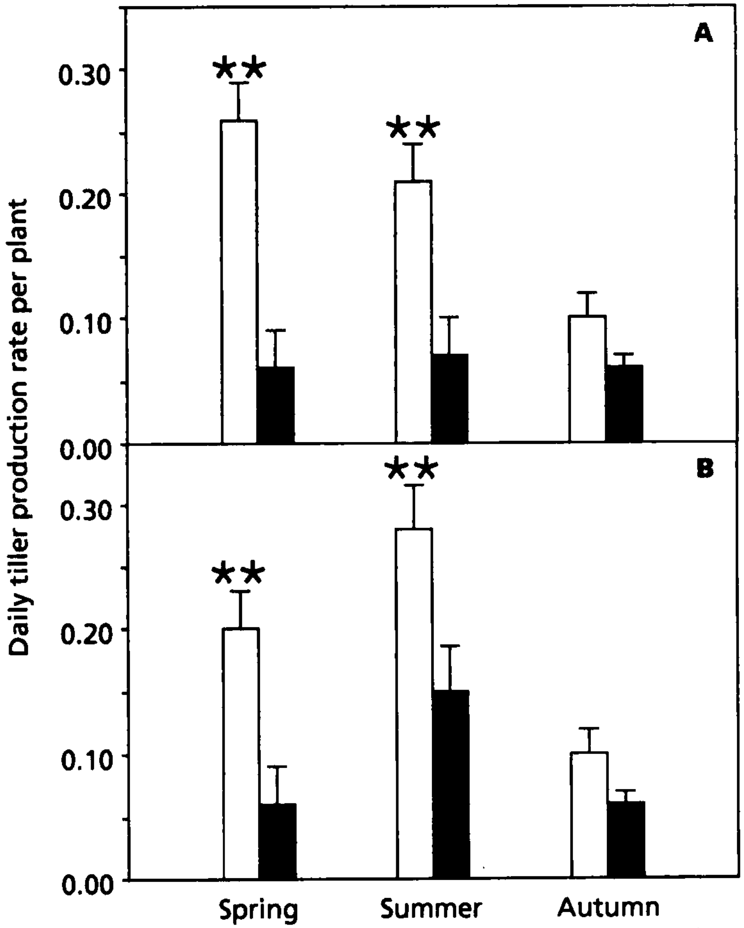


Fig. 2. Mean (± SE) daily tiller appearance rates for plants of (A) *Paspalum dilatatum* and (B) *Sporobolus indicus*. Plants were either grown with additional red light provided to the base of plants by red-light-emitting diodes (open bars) or controls (closed bars). Significant treatment differences ($p < 0{\cdot}01$) are indicated by asterisks. After Deregibus *et al.* (1985).

clear benefit in the high shoot densities of moss colonies. Because shoot height is very even, these colonies have a smooth surface, producing a boundary layer within which all of the shoots are "immersed". Under such circumstances, evaporation of water from the colony is limited by the boundary layer area of the colony rather than by the total area of leaves. For mosses that lack a cuticle, the advantage of reduced water loss outweighs the disadvantage of reduced irradiance, giving the highest productivity when shoots grow in dense stands.

C. Response to Soil Nutrient Status and Water Supply

Many of the studies relevant to this topic have been made on species with stolons and rhizomes. Experiments by Wareing (1964) and McIntyre (1976) on the rhizomatous *Agropyron (Elymus) repens* showed that many axillary buds do not grow when nitrogen is in low supply, but that provision of nitrogen stimulates the growth of laterals and the production of more branches (McIntyre, 1965; Williams, 1971). Low nitrogen supply causes growing axillary buds to develop as plagiotropic rhizomes, whereas application of nitrogen in various forms converts them into orthotropic tillers (McIntyre, 1967, 1976). Adequate water supply and high humidity promote lateral bud growth in *A. repens* (McIntyre, 1987) and in several other species (Hillman, 1984).

Results from other rhizomatous species confirm that higher nutrient levels stimulate the activation of lateral buds, but the effects on rhizome length are less consistent (Fig. 3). In a field experiment, Carlsson and Callaghan (1990) found that the tundra graminoid *Carex bigelowii* produced rhizomes with a greater mean length at higher fertility. However, this response was only significant for rhizomes initiated on the ventral (lower) side of the parent shoot base; rhizomes emerging from the dorsal (upper) side showed no significant response to fertilization. Schmid and Bazzaz (1992) showed that four old field perennials produced more, and shorter, new rhizomes in fertilized soil compared to unfertilized soil, but the length responses were mostly insignificant (Fig. 3). Internode lengths on rhizomes of *Hydrocotyle bonariensis* did not respond significantly to nitrogen supply (Evans, 1988, 1992), whereas petiole lengths increased. *Carex flacca* formed shorter rhizomes under a higher level of fertilization but the response was not significant; rhizomes of the grass *Brachypodium pinnatum* were significantly shorter under higher nutrient availability (de Kroon and Knops, 1990). Shoot height was also measured in these studies. All graminoid species increased in shoot height under a higher level of fertilization but to a variable degree. The especially vigorous response of *B. pinnatum* is likely to project leaves into the high light zone of the canopy and may contribute to its strong competitiveness under fertile conditions. In contrast, tiller length in *Deschampsia flexuosa* hardly responded to fertility, and tiller weight was greater at low fertility (Foggo, 1989). Foggo (1989) suggested that the formation of a limited number of large tillers may increase the competitiveness of *D. flexuosa* in the shaded, low fertility environments in which this species usually occurs.

Information about plasticity in response to nutrient levels in stoloniferous species corroborates the results described in the previous paragraph. Lateral bud development in the aquatic weed *Salvinia molesta* is almost completely suppressed when it is grown at low nutrient levels, but many second and third order branches are produced when nutrients are abundant (Mitchell and Tur,

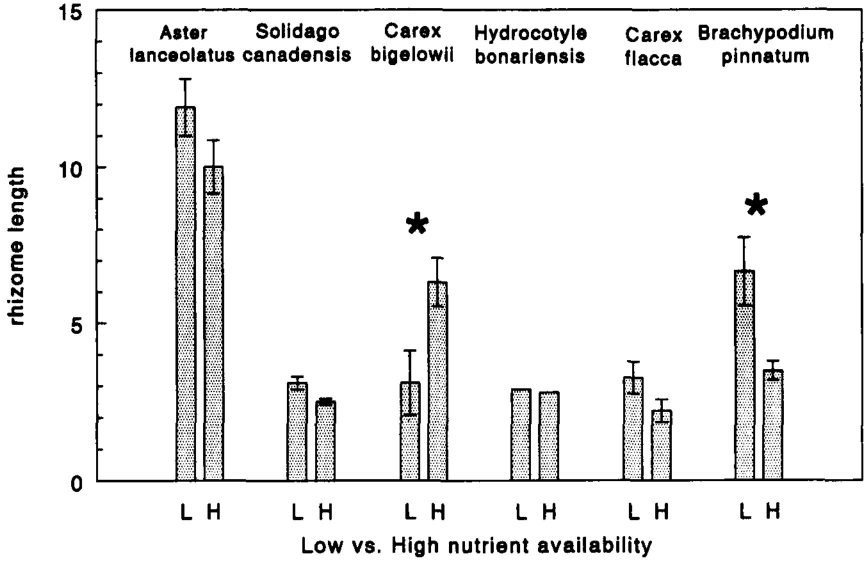


Fig. 3. Rhizome lengths of some herbaceous species under low (L) and high (H) nutrient availability. All values are means (± SE) in cm, unless indicated otherwise below. Significant treatment differences ($p < 0{\cdot}01$) are indicated by asterisks. Results of *Aster lanceolatus* and *Solidago canadensis* from a single season experiment in common garden soil in which the high nutrient plots received granular NPK fertilizer and the low nutrient plots remained unfertilized (Schmid and Bazzaz, 1992). Results of *Carex bigelowii* from a 3-year field experiment in which the high nutrient plots received an NPK nutrient solution three times a year and the controls received only water (Carlsson and Callaghan, 1990). Data for ventral rhizomes only. Error bars give 95% confidence limits. Results of *Hydrocotyle bonariensis* from single season experiment in sand (outdoors) in which the high nutrient treatment received nitrogen-augmented Hoagland solution and the low nutrient treatment received no nitrogen at all (Evans, 1992). Data for severed plants that received ample light and water. No standard errors are provided. Results of *Carex flacca* and *Brachypodium pinnatum* from a greenhouse experiment in a mixture of river sand and chalk soil fertilized with an NPK nutrient solution which was ten times more concentrated for the high than for the low nutrient treatment (de Kroon and Knops, 1990). Data for plants growing under high light only. *B. pinnatum* rhizome lengths in mm.

1975; Room, 1983; Julien and Bourne, 1986). A variety of species has been shown to branch far more when grown under higher nutrient availability (Ginzo and Lovell, 1973; Slade and Hutchings, 1987a; Hutchings and Slade, 1988; Evans, 1988, 1992; Alpert, 1991). Under such conditions, *Glechoma hederacea* produces shorter stolon internodes with a higher weight per unit length (Slade and Hutchings, 1987a), but internode lengths of *Ranunculus repens* (Lovett Doust, 1987) and *Fragaria chiloensis* (Alpert, 1991) did not respond to nutrients. *Trifolium repens* also branches more freely when nutrients are abundant, but produces *longer* internodes with a higher weight per unit length (Sackville Hamilton, 1982). However, Shivji and Turkington (1989) found similar stolon internode lengths in *T. repens* both in the presence and the absence of nitrogen-fixing bacteria. In many species the total length of primary stolons and their branches is almost independent of nutrient supply, although higher-order branching can be almost entirely suppressed at low nutrient levels (McIntyre, 1965; Ginzo and Lovell, 1973; Slade and Hutchings, 1987a; Hutchings and Slade, 1988).

D. Response to Competition

A number of authors have studied morphological plasticity in situations in which density or the level of competition varied naturally or were manipulated. While the observations can be relied on, there are difficulties in interpreting the morphological responses in terms of environmental conditions. For example, lower competition is not always associated with greater availability of nutrients, and it cannot be assumed that all other environmental variables remain constant as the level of competition changes. Light availability especially is likely to be higher in patches of habitat with lower density of plants. In heterogeneous field habitats there is also the difficulty that carryover effects from parts of the plant growing in good patches to parts growing in poor patches may cause the pure morphological response of the plant to its local growing conditions to be obscured (see Slade and Hutchings, 1987c). The effects described below must thus be treated cautiously.

S. Waite (unpublished) has shown that the internodes of *Ranunculus repens* stolons were significantly shorter on mole-hills devoid of vegetation than elsewhere in a meadow habitat. This observation contrasts with the results of the greenhouse studies on this species which were reported above. Eriksson (1986) found no effect of density upon internode lengths in *Potentilla anserina*. Bishop and Davy (1985) observed more stolon branching in *Hieracium pilosella* grown at lower density. *Lycopodium annotinum* branches more in sites where nitrogen-fixing lichens are present (Svensson and Callaghan, 1988), and *Solidago canadensis* clones produce fewer but longer rhizomes when grown experimentally at greater density (Hartnett and Bazzaz, 1985). However, four old-field perennials, including *S. canadensis*, tended to produce more and shorter rhizomes when grown together with species in which rooting density was higher (Schmid and Bazzaz, 1992). It was suggested that this result may have been due to mechanical resistance of dense root mats to penetration by rhizomes. *Glechoma hederacea* stolon internodes and petioles were significantly longer when grown in competition with uncut swards of *Lolium perenne* than when growing without competition (E.A.C. Price and M.J. Hutchings, 1993, unpublished). The effect on petiole lengths was especially strong. In competition with grass swards cut to 1 cm height, however, stolon and petiole lengths were not significantly different from those on the control clones. However, the total biomass of the *G. hederacea* clones was equally reduced by the competition treatments involving uncut and cut grass swards.

E. Response to Stress

Under some environmental conditions essential resources (light, water, mineral nutrients) may be available in ample quantities but some other factor restraining growth limits their uptake by the plants. Under such circumstances, plants may invoke morphological responses which promote escape from these conditions. Resource-acquiring structures may then be non-randomly placed into microsites from which essential resources can be obtained more efficiently. Examples of such foraging responses are presented in the following paragraphs.

1. Response to Flooding

Flooding prevents adequate diffusion of gases between plants and the atmosphere, often leading to death of the plant. Elongation of immersed shoots out of the water, together with an increase in aerenchymatous tissue in roots during flooding, promotes the diffusion of oxygen from the shoots to the root tips, and is a well-documented response which can promote survival (e.g. Voesenek and Blom, 1989; Laan and Blom, 1990; Waters and Shay, 1990). The elongation response is caused by an increased synthesis of ethylene, and reduced diffusion of ethylene from within the plant to the atmosphere, which results in an increase mainly in cell expansion but in some cases also in cell division (Voesenek *et al.*, 1990). Stem elongation can also be stimulated by external application of ethylene to non-immersed plants (van der Sman *et al.*, 1991), whereas immersion of the plant in a solution of silver nitrate (an inhibitor of ethylene action) inhibits elongation (Voesenek and Blom, 1989). Species with a higher tolerance of flooding show greater responses to shoot immersion, with both developed parts and newly forming parts elongating, whereas flooding-intolerant species show small responses which are confined to newly produced parts. The responsiveness of the plant also alters as it moves through different developmental phases.

2. Response to Burial

Shoot height also increases in a saltatory fashion following burial in sand, as shown by Seliskar (1990) in *Scirpus americanus*. Whether this is due to an etiolation response in tissue formed in the dark during burial, or to an increase in ethylene concentration within the plant, is not known.

3. *Response to Salinity*

Salzman (1985) found that whereas salinity strongly limited biomass accumulation in *Ambrosia psilostachya*, ramet dispersal was greater under saline than non-saline conditions. She interpreted this result as an expression of a commitment to extensive rhizome spread, which increased both the rate at which plants explored new territory and the probability of encountering more favourable habitat.

4. *Response to Touch*

When *Arabidopsis thaliana* is stimulated by touch, it develops shorter leaves and longer stems (Braam and Davis, 1990). Calcium ions and calmodulin are involved in transduction of signals from the environment, enabling plants to sense and respond to environmental change. If the responses to touch were induced by neighbouring plants, they could result in stem etiolation, which might overtop these neighbours and reduce physical interference from them.

F. Response to Host Quality by Parasitic Plants

Those plants which are heterotrophic depend on resources which are available in discrete patches (host plants) within a background environment which provides no resources at all. Like foraging animals, parasitic plants thus make decisions about whether or not to exploit patches of resources, and about when to leave them, having extracted a certain amount of resources. Kelly (1990) examined these questions in *Cuscuta subinclusa* and showed that stems coiled more on hosts which gave a higher yield of resource per unit of coil length. Thus, the parasitic plant was capable of assessing the quality of the host prior to resource uptake. The level of investment in coiling upon the host depended on the expected reward, measured in amount of resource acquired. The coiling cues are as yet unclear. No relationship was found between coiling and host nitrogen content, and it was suggested that host flavonoid levels mediated the coiling response. However, in a later study with *Cuscuta europaea* Kelly (1992) did find that stems were more likely to accept (i.e. coil upon) hosts of higher nutritional value.

G. The Mechanism of Morphological Plasticity in Shoots

The shape of a plant both above- and below-ground is a product of the differential activity of meristems. Each actively growing apex completely or partially inhibits the development of lateral structures derived from the same or different apices. This is known as correlative inhibition. In orthotropic shoots the highest lateral buds are usually the first to grow out following decapitation of the apex; in plagiotropic shoots it is the laterals nearest the roots which develop preferentially following this treatment (Hillman, 1984). It is well-documented that major factors which influence plant morphology include the effects of plant growth substances and phytochrome on apical dominance and internode elongation. Here we briefly review what is known about these regulation mechanisms.

Matthysse and Scott (1984), Tamas (1987) and Woodward and Marshall (1988) have provided succinct accounts of the effects of plant growth substances on axis elongation and lateral bud growth on stems, tillers and roots. Auxins, cytokinins and gibberellins appear to be the most important of the plant growth substances in shaping gross morphology. Auxins are synthesized mainly in shoot meristems and expanding leaves, cytokinins in the roots, and gibberellins in both shoots and roots. Auxins impose apical dominance in shoots and inhibit the growth of tillers and lateral buds on stems, but they promote branching in the root system. Cytokinins and their analogues promote the growth and development of shoot branches and tiller buds, and appear to impose apical dominance in the root system (Johnston and Jeffcoat, 1977; Sharif and Dale, 1980; Jinks and Marshall, 1982; Tamas, 1987), but the evidence for this is debatable (Hillman, 1986; Roberts and Hooley, 1988). Gibberellins promote main stem development and reduce the development of tiller buds (Jewiss, 1972; Johnston and Jeffcoat, 1977; Isbell and Morgan, 1982; Woodward and Marshall, 1988). However, their application to root systems may result in the release of buds from apical dominance (Watson *et al.*, 1982), probably because root apex growth is inhibited (see also Tamas, 1987). Matthysse and Scott (1984) suggest that auxins and cytokinins are important in controlling rapid responses by plants to short-term, unpredictable fluctuations in growing conditions, whereas gibberellins govern responses to gradual changes, such as those taking place over the course of a season.

There are now strong arguments for auxins, and in particular for the active substance indole-acetic acid (IAA), being a signal which directly or indirectly suppresses the activity of lateral meristems (Hillman, 1986; Tamas, 1987; Roberts and Hooley, 1988; Tamas *et al.*, 1992). Cytokinins transported from roots to shoot are probably needed for the activity of lateral buds, but the expression of the activity may be under apical control (Tamas, 1987). The patterns of water and nutrient distribution throughout the plant play a role in apical dominance, but possibly *via* hormone-directed metabolite transport (Hillman, 1984; Salisbury and Marinos, 1985). Shein and Jackson (1972) suggested that the growth of laterals and main stems depends upon a complex hormone balance which could be modified by several internal and external factors including water and nutrient status, light regime and plant age. A delicate interaction may exist between auxins, gibberellins and cytokinins, producing the degree of apical dominance which is expressed in the phenotype (Jewiss, 1972; Woolley and Wareing, 1972; Woodward and Marshall, 1988).

Scarcity of nutrients and water normally result in stronger apical dominance (Gregory and Veale, 1957; Phillips, 1975; Hillman, 1984; Salisbury and Marinos, 1985) and there is a positive relationship between both soil nutrient availability (especially nitrogen supply) and water supply, and cytokinin synthesis (Aung *et al.*, 1969; Banko and Boe, 1975; Menhenett and Wareing, 1975; McIntyre, 1976; Qureshi and McIntyre, 1979; Menzel, 1980; Lovell and Lovell, 1985). The effect of nitrogen application on the propensity of rhizome buds to grow out as orthotropic tillers rather than plagiotropic rhizomes, as reported in a previous section, may be due to a combined effect of low levels of IAA and high levels of gibberellic acid (Bendixen, 1970; see Hutchings and Mogie, 1990). However, in general there is little information about the effects of environmental conditions upon the concentrations of plant growth substances, except for hormones that seem to be less important for the control of apical dominance, such as abscisic acid (e.g. Davies and Zhang, 1991). Together with the fact that most of the work on this subject has been carried out with a restricted group of legume and grass species, this lack of information hinders an interpretation of the effects of the environment on morphology in terms of the actions of growth substances.

Changes in shoot morphology in response to light quality operate through photochemical changes in the state of phytochrome, the main sensor of shade light quality. The degree to which a stem elongates depends on the ratio between P_{fr}, the active form of phytochrome, and the total phytochrome content, P_{total}. High rates of stem extension take place when no P_{fr} has been formed, as in seedlings growing towards the soil surface immediately after germination. The low R/FR ratio of light which has passed through a plant canopy reduces the photoequilibrium, P_{fr}/P_{total}, compared with plants in the open, thus promoting stem elongation. The shade cast by plant canopies in terrestrial communities causes changes in the value of the R/FR ratio over a range within which the photoequilibrium is highly unstable. The ratio of P_{fr} to P_{total} can thus provide a very sensitive indication of the presence of shade and the degree of shade cast (Smith, 1982; Holmes, 1983). It is, however, far more stable at R/FR ratios above 1·5. The R/FR ratio increases rapidly with passage of light through water, and for this reason the photoequilibrium is unlikely to be sensitive enough to operate as a sensor of shade cast by plant leaves in aquatic habitats (Smith, 1982). Artificial manipulation of the ambient R/FR light regime can dramatically change plant morphology, as already discussed (Casal *et al.*, 1985; Deregibus *et al.*, 1985). Imposition of very high R/FR ratios promotes vigorous branch production by roses and tomatoes even when they are grown at densities at which severe mutual shading occurs (Novoplansky *et al.*, 1990b). Flowering and fruiting can also be increased spectacularly by such treatment.

Phytochrome does not seem to affect internode elongation directly. It appears to act indirectly *via* gibberellin. Localized shading of stems promotes stem elongation by inducing greater rates of cell division and expansion (e.g. Garrison and Briggs, 1972 for *Helianthus*), and these responses have traditionally been regarded as an expression of altered gibberellin metabolism. Indeed, when gibberellic acid is applied to *Xanthium* internodes, rates of cell division and elongation increase and the growth rate in internode length more than doubles compared to control plants (Maksymowych *et al.*, 1984). Recent research suggests that in darkness or under low R/FR ratios phytochrome alters the sensitivity of the stem tissue to gibberellic acid, thus enhancing the ability of internodes to elongate (Garcia-Martinez *et al.*, 1987; Martinez-Garcia and Garcia-Martinez, 1992; Ross and Reid, 1992).

Photon flux density also affects shoot morphology, but the mechanisms by which the effects are exerted have received little attention. It is thought that some species sense changes in photon flux density *via* blue light photoreceptors (Holmes, 1983). The responses, which again result in increased stem extension rates, are fast, but in many cases limited to the earliest stages of growth (the hypocotyl stage). It is believed that such responses may allow the young plant to avoid small obstacles such as stones and mounds of soil (Holmes, 1983).

H. Preferential Shoot Proliferation in Favourable Patches

Most habitats are heterogeneous, consisting of patches which differ in resource availability. In low vegetation, above-ground patchiness may be imposed by the spatial arrangement of dwarf shrubs and persistent clumps of perennial herbs (e.g. Eriksson, 1986; van der Hoeven *et al.*, 1990), and modified by micro-topography and grazing (Gibson, 1988a; Svensson and Callaghan, 1988). Forest canopies are patchy because of gaps and because tree species with different architectures and light transmission properties occur together. Here we review studies which have looked at the selective placement of shoots, and of the leaves on shoots, within the patchy environment, rather than at morphological plasticity itself.

The probability of buds growing out, and of leaves and branches being produced at any node, varies with local site quality. For example, Jones and Harper (1987a,b) showed that fewer buds developed in parts of *Betula pendula* crowns with high local shoot densities and presumably low light. A similar regulatory effect was seen regardless of whether crowding was caused by shoots of the same plant or shoots of a different plant. As a consequence, trees grown in isolation develop symmetrically, but when grown close together they show a strong tendency to grow more on those sides which face away from neighbours (Franco, 1986; Young and Hubbell, 1991). Weiner *et al.* (1990) showed that branch distribution up stems differed between isolated and competing plants of *Impatiens pallida*. Isolated plants produced branches from lower on the main stem, and more second-order branches, than crowded plants. The vertical distribution of first- and second-order branches on isolated plants was the same, but competing plants produced second-order branches only from their highest first-order branches. Suppressed competing plants produced branches and leaves only at the top of their stems, where access to light would be greatest. Thus, probability of formation of branches depended on the favourability of local conditions.

The capacity to concentrate in light patches in a heterogeneous environment appears, at least in bryophytes, to be greater for species with a high relative growth rate under uniform conditions, and for species of open rather than shaded habitats (Rincon and Grime, 1989). However, During (1990) suggested that this observation may be a consequence of the differences in growth form between the species that Rincon and Grime used (acrocarps *versus* pleurocarps), rather than due to differences in growth rate or habitat.

When light patchiness is created by the placement of leaves and shoots of competing plants, the responses of species to environmental patchiness may have consequences for the competitive interactions between species. Recent experiments have shown that the success of the most dominant species of herbaceous phanerogams in gaining access to good habitat patches appears to be primarily due to their ability to rapidly develop a large mass of leaves (and roots) in those patches (Campbell *et al.*, 1991a,b). However, the percentage of leaf and shoot weight increments which individual species achieve in light-rich patches under heterogeneous experimental conditions is negatively correlated with their proportional contribution to the total biomass of a mixture of competing species. In other words, subordinate species show greater *precision* than dominant species in locating the more favourable patches (Campbell *et al.*, 1991b). It seems therefore that dominant species produce large leaf and root masses in both good and poor quality habitat patches, while subordinate species have a greater capacity to select the better patches. As this placement is achieved by morphological plasticity, it may be hypothesized that subordinate species may have more plastic shoot architectures than dominant species. To our knowledge data with which to test this hypothesis are lacking. Greater selectivity in the placement of resource-gathering structures in higher quality habitat patches may be an important attribute enabling less competitive species to avoid competitive exclusion from mixed communities.

Many species with plagiotropic stems do not shorten their internodes under more favourable conditions (Figs. 1, 3). Such species would therefore not be expected to concentrate the placement of their ramets in favourable patches as a result of morphological plasticity. Even stoloniferous species with qualitatively similar internode length responses to those of orthotropic shoots are inefficient at placing ramets in resource-rich patches, as demonstrated recently by Birch and Hutchings (1994). Clones of *Glechoma hederacea* growing under heterogeneous nutrient supply produced shorter internodes in nutrient-rich patches, but the density of ramets in these patches was hardly altered by this response. This result is confirmed by model simulations in which the distribution of ramets of *G. hederacea* in a patchy environment was calculated on the basis of its morphological responses (Cain, 1994). The degree of plasticity of plagiotropic stems therefore may not be sufficient to result in a marked concentration of ramets in favourable patches of habitat, in contrast to the predictions of the models of Sutherland and Stillman (1988, 1990).

The speed with which an internode ceases to elongate has great significance for foraging. Once internode elongation has stopped, the node at its apex is fixed in position and leaves and (in plagiotropic stems) roots are produced from this site. Rapid fixation of the position of the node allows resource uptake to commence quickly. For example, Birch and Hutchings (1992) and Dong (1993) found that stolon internodes in two stoloniferous species reached their final lengths rapidly. When a ramet at the end of a fully elongated stolon internode is in a nutrient-rich patch, *Glechoma hederacea* exploits the nutrients by very rapid development of roots from that ramet (Birch and Hutchings, 1994); when the ramet is in a poor patch, however, its roots begin to develop later, and root growth is much less profuse. In marked contrast to the rapid completion of internode growth, a protracted period of growth of petioles, and of the leaf lamina, allows the plant to make ongoing responses to unfavourable or deteriorating light conditions long after the position of the ramet has been fixed on the soil surface (Birch and Hutchings, 1992; Dong, 1993).

I. Conclusions

The data show that all orthotropic stems and stem analogues (such as leaf sheaths) respond similarly to variations in light quantity and quality; under a more favourable light regime branching increases and internode elongation decreases. The *degree* of plasticity differs between species, however, and there is evidence that the response is greater in shade-intolerant than shade-tolerant species. This response to canopy shade provides orthotropic shoots with some capacity to overgrow competitors for light, but this will be of little value for species of short stature in habitats in which most of the shade is cast by canopy trees.

While plagiotropic and orthotropic stems respond similarly to light with respect to branching by lateral meristems, comparison of the responses of internode lengths is less straightforward. Some species with plagiotropic stems exhibit reduced internode lengths under more favourable light conditions, but lack of a response, and even an increase in internode lengths have been reported for others. The responses to variations in nutrient availability are equally inconsistent. Even when species with plagiotropic stems do shorten their internodes under more favourable nutrient conditions, the degree of plasticity which has been reported appears to be too small to concentrate ramets efficiently in the high quality patches in the habitat. An understanding of the differences in response to environmental quality between orthotropic and plagiotropic stems is hindered by a lack of information about the interactive effects of the environment and plant growth substances on stem elongation.

V. THE FORAGING ACTIVITIES OF ROOTS

Root morphology can be described in terms of the density of formation of laterals and the rate of root extension, and also in terms of the topology of the branching system. Both types of description are used here to review the plastic responses of roots to variation in the availability of soil resources. This material is supplemented with information on the proximal mechanisms that control the responses of roots. In a final section we investigate the effectiveness of roots at exploiting patches of high nutrition within the soil volume, and the consequences for plant growth.

A. Plasticity in Root Branching and Elongation

The distinction between resource-acquiring structures and spacers is not as clear-cut in roots as it is in stems. Edaphic resources (water, nutrients) are taken up all along the root surface, but the younger, finer roots and the terminal zones bearing root hairs are the most important areas for these activities (Passioura, 1988). Root extension increases both the area of the absorbing surface and the volume of soil explored. Local root surface area can be increased by lateral root branching.

Unlike stems and stem homologues, roots do not have a segmented metameric construction (Steeves and Sussex, 1989; but see Barlow, 1989). In angiosperms, lateral root primordia originate in the pericycle—the outermost cell layer of the stele—and arise in ranks (orthostichies) which are usually positioned opposite the protoxylem poles of the vascular system (Lloret *et al.*, 1988; Steeves and Sussex, 1989). The longitudinal spacing of lateral roots usually has some degree of regularity. The number of lateral roots in each of the ranks can vary widely. Lateral roots are usually initiated at a certain distance from the root tip and branching does not occur on older parts of roots (Drew *et al.*, 1973; Lloret *et al.*, 1988), although dormant root primordia as well as the formation of 'adventive' roots are reported for some species (see Barlow, 1989).

The fact that branching of roots may be stimulated under higher levels of soil nutrition was recognized as early as the late 1800s (see Wiersum, 1958). Weaver (1919) produced numerous diagrams showing that roots proliferated selectively in pockets of soil that were rich in soil resources. Drew *et al.* (1973) were among the first to experimentally study the effects of local nutrient enrichment on root morphology. Single root axes of barley (*Hordeum vulgare*) were grown into three compartments in which the concentration of nutrients could be controlled separately. High nitrate concentration in a given compartment promoted the formation of more first and second order laterals per unit of primary root length within that compartment, and greater lateral root extension (Fig. 4). These responses were significant irrespective of the level of nutrition experienced by other parts of the root system. In contrast to the growth of the lateral roots, the rate of extension growth of the main root axis was *not* affected by nitrate availability in the compartment in which it was growing. These results were essentially corroborated by later work (Drew, 1975—see Fig. 4; Drew and Saker, 1975, 1978; Eissenstat and Caldwell, 1988a; Granato and Raper, 1989; Jackson and Caldwell, 1989; Burns, 1991). Caldwell and his co-workers examined the extension growth of roots in three cold desert perennials, making no distinction between main root axes and laterals. Local enrichment of the soil by injection with a nutrient solution significantly stimulated root elongation at different times of the year (Eissenstat and Caldwell, 1988a). Species differed markedly both in the degree to which root growth was stimulated and in the time between nutrient application and response. *Agropyron desertorum* showed a fourfold increase in the relative growth rate of root length within one day, while *Artemisia tridentata* and especially *Pseudoroegneria spicata* responded less vigorously (Jackson and Caldwell, 1989). In the latter species extension growth was not affected until several weeks after nutrient application. It is likely that the root growth of *A. desertorum* also responds more strongly to water availability than the root growth of the other two species, because roots of *A. desertorum* can more rapidly invade disturbed soil patches which are not enriched in nutrients (Eissenstat and Caldwell, 1989), and because this species is a stronger competitor for water (Eissenstat and Caldwell, 1988b).

The mobility of nutrient ions in soil may differ by several orders of magnitude. Diffusion coefficients decline from nitrate to ammonium to phosphate (Nye and Tinker, 1977; Caldwell, 1988). Bray (1954), Harper (1985) and Fitter (1991) hypothesized that root morphological characteristics may depend on the diffusive properties of the nutrient for which the plant is foraging. Prolific branching producing a high root density would seem to be required for effective acquisition of immobile ions such as phosphate. For nitrate a less intensive branching pattern should suffice. However, there is little evidence to show that the morphology of roots depends on the type of nutrient which is in short supply. Drew (1975) found that the nitrate, ammonium and phosphate anions were equally effective in inducing lateral

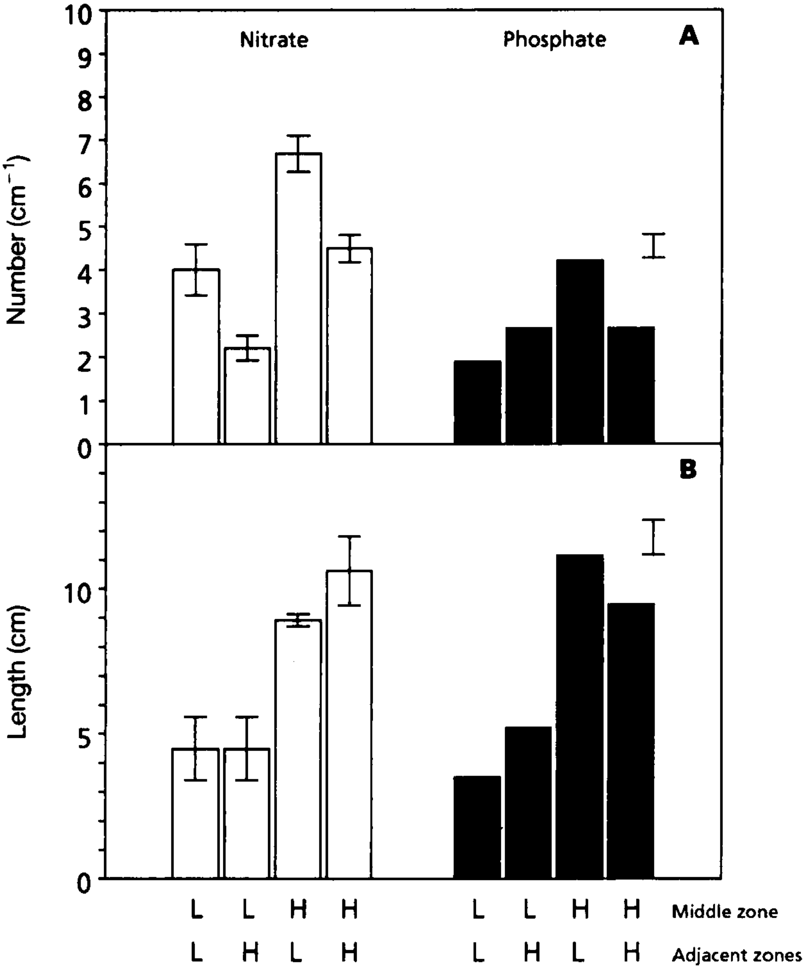


Fig. 4. Effects of nitrate and phosphate supply on (A) the numbers of lateral roots per cm of main root axis, and (B) the lengths of individual lateral roots in barley. Main root axes were divided into three zones and nutrients were supplied independently to each of these zones. Data given are those for the first-order laterals that developed in the middle zone. This zone experienced either a low (L) or a high (H) concentration of nitrate or phosphate. Adjacent rooting zones also grew in either low or high nutrient solution. In the nitrate experiment plants were grown hydroponically. In the phosphate experiment they were grown in sand. Nitrate data given as means ± SE, phosphate data as means with separate bars showing the LSD at the 5% level. After Drew *et al.* (1973) (nitrate) and Drew (1975) (phosphate).

root formation and growth (see Fig. 4), while potassium availability had no effect. Wiersum (1958) grew roots over ion adsorbing resins and reported a larger effect of nitrate than of other ions on root branching. However, he also failed to demonstrate an effect of cations. In contrast, Passioura and Wetselaar (1972) suggested that the concentration of roots of wheat in the soil corresponded more closely with the distribution of ammonium than of nitrate, while roots of birch displayed no preference for either form of nitrogen (Crabtree and Bazzaz, 1992). Jackson and Caldwell (1989) showed that an increase in root extension could be induced by N–P–K fertilization as well as by N and P alone, and that the magnitude of the response was a function of the level of enrichment. Ion specificity in the responses of roots may be lacking because in reality roots always forage for multiple resources simultaneously.

In comparison with the diameter of stems, root diameter shows little plasticity. In many species, specific root length (SRL, root length per unit root dry weight) does not change significantly as a function of nutrient availability. In species which do respond, SRL is always higher under more nutrient-poor conditions (Fitter, 1985; Robinson and Rorison, 1985, 1987, 1988; Boot and Mensink, 1990; Hetrick *et al.*, 1991). Thus, when nutrients are scarce, thinner roots are formed, which explore the soil more efficiently (Nye, 1973) at lower cost.

B. Plasticity in Root Topology and Architecture

A different way of examining root morphology is the topological analysis of branching pattern introduced by Fitter (Fitter, 1986, 1987, 1991; Fitter *et al.*, 1991). Roots are divided into a number of "links", where a link is defined as a root segment between either two branch junctions or nodes (internal link) or between a branch junction and an apex (external link). The branching pattern of a root system is typified by a number of parameters such as the total number of external links and the maximal and total path lengths of the external links to the base (origin) of the root system. Additional (non-topological) parameters include link length and branch angles. Using this approach, Fitter (1986) described the plasticity of roots of *Trifolium pratense* in response to water availability. Under drought the root system was characterized by linear growth and internal branching giving rise to a herringbone type of structure. Abundant soil moisture resulted in predominantly external branching and a more dichotomous structure. Increasing water availability increased the external link length (indicating that branch initiation occurred further behind the growing tip of the root), but interior link length was unaffected. Subsequent studies with a variety of other species showed roughly similar responses of root morphology to different levels of nutrient availability (Fitter *et al.*, 1988; Fitter and Stickland, 1991; Fitter, 1993, 1994).

Internal and external link lengths were usually lower when nutrient availability was greater but some species showed the opposite responses (Fitter and Stickland, 1992). In general, the levels of plasticity shown by individual species were small compared to the differences in root topology between species. A number of species (including all of the grass species studied) did not respond significantly to different levels of edaphic resources. Species in the same genus frequently behaved in a similar way, suggesting that root architecture is partly determined by phylogeny (Fitter and Stickland, 1991).

Fitter *et al.* (1988) showed that species from poor soils generally had a more herringbone root structure with longer links than species from rich soils, but this conclusion was only partly corroborated by the results of a subsequent study (Fitter and Stickland, 1991). The larger soil volume occupied by the roots of species from relatively nutrient-poor habitats may be important for acquiring scarce resources. Hence, species-specific root architecture may have greater functional significance than morphological plasticity (Fitter, 1991).

Topological characterization of the entire root system appears to be less sensitive than measurements of root branching and root extension rate for reflecting responses to variation in resource supply (see previous section). Thus, topological analysis carried out by itself may obscure some of the morphological plasticity of which roots are capable.

C. Effects of Infection by Mycorrhizal Fungi

Infection by arbuscular mycorrhizal (AM) fungi may significantly alter root morphology and plasticity. Mycorrhizal hyphae play an important role in the uptake of some nutrients, and may effectively take over the role of the fine roots and root hairs. Inoculation of roots with AM fungi has been shown to reduce root branching, lateral root extension and the development of root hairs (Steeves and Sussex, 1989; Hetrick *et al.*, 1991). The morphology of infected roots responds weakly to differences in nutrition compared to uninfected roots (Hetrick *et al.*, 1991). St John *et al.* (1983a) grew inoculated plants in pots with soil patches of different quality. It was shown that total hyphal length was significantly higher in patches rich in organic matter compared with patches containing only sand. This was probably caused by increased branching of hyphae in the nutrient-rich patches. Thus, branching of mycorrhizal hyphae seems to respond to local variations in soil nutrients in a similar way to the branching of roots reported above (St John *et al.* 1983b; see also section VI on the foraging activities of fungi).

D. The Mechanism of Morphological Plasticity in Roots

The root tip exerts an inhibiting effect on the development of lateral roots, comparable with the way in which the shoot apex suppresses the development of lateral structures. Hence, root branching is stimulated by removal or death of the root tip (Lloret *et al.*, 1988; Callaway, 1990). It has been suggested that, in principle, every cell in the pericycle is capable of lateral root formation (Barlow, 1989). The regular placement of lateral roots seems to be the result of the interplay between an inhibiting effect on branching caused by the apex and a promoting effect which develops in mature regions of the root (Lloret *et al.*, 1988). In addition, existing lateral roots may have an inhibiting influence on the formation of new laterals (Steeves and Sussex, 1989).

The general effects of plant growth substances on apical dominance have been discussed in the section on the foraging activities of shoots. Much less is known about the regulation of apical dominance in the root than in the shoot. Granato and Raper (1989) suggest that, when nitrate levels in the substrate are low, inhibition of lateral root formation may be due to a reduction of nitrate reductase activity in the root tip which in turn reduces the concentration of organic nitrogen compounds. This may explain the responses of branching to availability of nitrate, but not to other nutrients. It is not clear why lower levels of nutrition usually reduce the extension growth of lateral roots but not that of the main axis. One reason may be that the primary root apex is stronger than the lateral root apices as a sink for carbohydrates and reduced nitrogen compounds (Granato and Raper, 1989).

E. Preferential Root Proliferation in Favourable Patches

In many habitats the spatial distribution of water and nutrients is profoundly heterogeneous even at a scale as small as a few centimetres (Frankland *et al.*, 1963; Hall, 1971; Gibson, 1988a; Svensson and Callaghan, 1988; Lechowicz and Bell, 1991). For example, Jackson and Caldwell (1993) recently found that nitrate and ammonium concentrations in the soil of a cold desert habitat varied more than tenfold at a scale of 50 cm, and that there was still a threefold variation at a scale of 3 cm. Soil patches of different quality may be created at these scales by abiotic factors (soil type differences, soil depth, micro-topography) as well as by biotic factors such as treefalls and stemflow in forests (Lechowicz and Bell, 1991) and persistent turfs of perennial plants in grasslands and deserts (Gibson, 1988a,b; Hook *et al.*, 1991; Jackson and Caldwell, 1993). How effectively are roots placed in the richer patches within the soil volume, and to what extent can the resources in these patches actually be acquired? What fraction of the growth achieved under a homogeneous supply of soil resources can be realized when similar amounts of resources are patchily distributed?

Caldwell *et al.* (1991a) locally enriched soil in a cold desert habitat and showed that within 3 weeks *Agropyron desertorum* had developed a higher root density in patches of soil supplied with nutrients than in control patches that received only water (Fig. 5A). This concentration of roots was probably

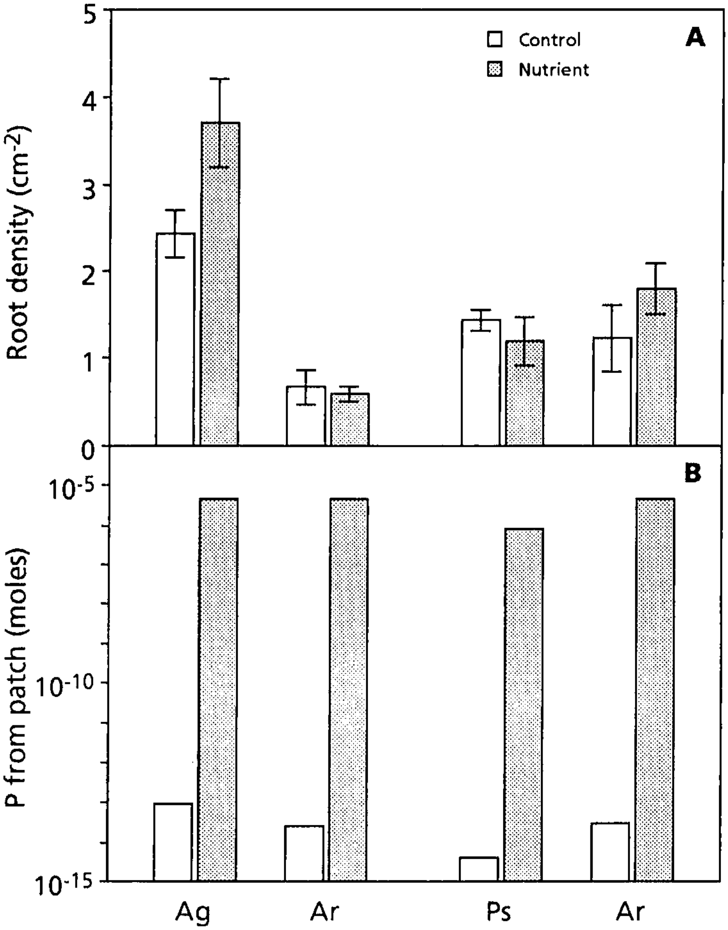


Fig. 5. (A) Root density and (B) phosphate uptake in a field experiment in which soil cores were either enriched with an NPK nutrient solution or supplied with distilled water (controls). Roots of two pairs of species were allowed to grow into the cores simultaneously, in two combinations: *Artemisia tridentata* (Ar) competed with either *Agropyron desertorum* (Ag) or with *Pseudoroegneria spicata* (Ps). The experiment lasted for 5 weeks; root data came from a harvest after 3 weeks. Root density is the number of root intersections in cut planes of soil cores. Note log scale in B. After Caldwell *et al.* (1991a,b).

the result of vigorous root extension growth in response to nutrient enrichment, as reported for this species by Jackson and Caldwell (1989). The uptake of phosphorus was orders of magnitude higher from the enriched than from control soil patches (Caldwell *et al.*, 1991b) (Fig. 5B). This was partly due to the aggregation of roots, and partly a result of higher rates of phosphorus uptake per unit of root length, in enriched patches of soil (Caldwell *et al.*, 1992). In contrast to *A. desertorum*, two other species, *Pseudoroegneria spicata* and *Artemisia tridentata*, proliferated roots equally in fertilized and control patches (Fig. 5A), but exhibited higher phosphorus uptake rates in the enriched patches. In a subsequent study (Van Auken *et al.*, 1992) it was shown that *Artemisia tridentata* and *Agropyron desertorum* were more capable than *P. spicata* of exploiting distant soil microsites enriched in phosphate. This was probably a result of the higher root extension growth of the former species.

De Jager and Posno (1979) compared the root growth of three *Plantago* species in a split-root experiment in which phosphorus was withheld from most of the root system. *P. major*, a species from relatively nutrient-rich sites, proliferated roots more rapidly in soil compartments supplied with ample phosphorus than *P. media*, a species from relatively nutrient-poor habitats. The response of *P. lanceolata* was intermediate to the other two species.

Crick and Grime (1987) grew plants of *Agrostis stolonifera* and *Scirpus sylvaticus* in arenas in which their roots could be equally distributed between several compartments. The strength of the nutrient solution provided in each compartment could be controlled independently. In addition to uniform high and low nutrient treatments to all compartments, nutrients were applied either in a stable configuration to particular compartments or as pulses applied consecutively to selected compartments. After 27 days of growth, root dry weight of *A. stolonifera* was markedly higher in compartments with a high nutrient supply for the duration of the experiment than in compartments with a low nutrient supply. In contrast, roots of *S. sylvaticus* did not accumulate preferentially in high nutrient compartments. Crick and Grime (1987) interpreted the differences in responsiveness between the species as adaptations to habitats with fertile (*A. stolonifera*) and infertile soils (*S. sylvaticus*). More recently, Grime *et al.* (1991) were unable to repeat this result with seedlings of 11 species grown in pots of sand divided into sectors with low and high nutrient supply, although there were no physical barriers between sand of different quality in this experiment. The extent to which roots developed preferentially in the richer sectors of the soil was similar for species from both fertile and infertile habitats. Fast-growing species developed a higher biomass than slow-growing species not because they placed more roots in nutrient-rich sectors, but probably because their nutrient uptake rates were higher (see also Section VIII.A and Fig. 9).

An experimental study referred to earlier, by Drew *et al.* (1973) analysed the effects of local nutrient enrichment upon root morphology in barley. It also analysed the effects of local nutrient enrichment upon the localization of root growth. It involved subjecting different fractions of the root systems of plants to either high or low nutrient supply provided in separated compartments. When one-third of the entire root system received a nutrient-rich solution, total lateral root length per unit of length of the primary axis was ten times higher, and the total root biomass six times higher, in the high nutrient compartment than their values in the low nutrient compartments. Later in the experiment, when the lateral roots had grown out, whole plant relative growth rate (RGR) under localized supply of nutrients approached the value attained by control plants growing under homogeneous nutrient supply (Drew and Saker, 1975). When phosphate was supplied to 2 cm of the main root axis—a fraction amounting to only a few per cent of its total length—whole-plant RGR was more than 80% of its value in control plants in which the whole root system received phosphate. When applied to 4 cm of the main root axis, the RGR for the whole plant was similar to that of controls. There were increased lengths of lateral roots, and increased phosphate absorption rates per unit of root length in the enriched compartment, compared with both other parts of the root system in treated plants, and the root system of control plants (Drew and Saker, 1975). Similar results have been obtained in split-root experiments with maize (de Jager, 1982) and lettuce (Burns, 1991).

Birch and Hutchings (1994) grew clones of *Glechoma hederacea* in flats in which a given amount of potting compost was either uniformly mixed with sand or confined to a circular patch occupying only 11% of the total area of the flat. Due to vigorous rooting within the high nutrient patch, total clone biomass in the heterogeneous treatment was more than twice as high as in the treatment in which the nutrients were uniformly distributed (see Fig. 8).

The results of these studies show that high nutrient patches can be rapidly occupied by species with morphologically responsive root systems. For such species whole plant growth in a patchy environment can be similar to, or even higher than in an environment in which the same supply of resources is uniformly distributed.

F. Conclusions

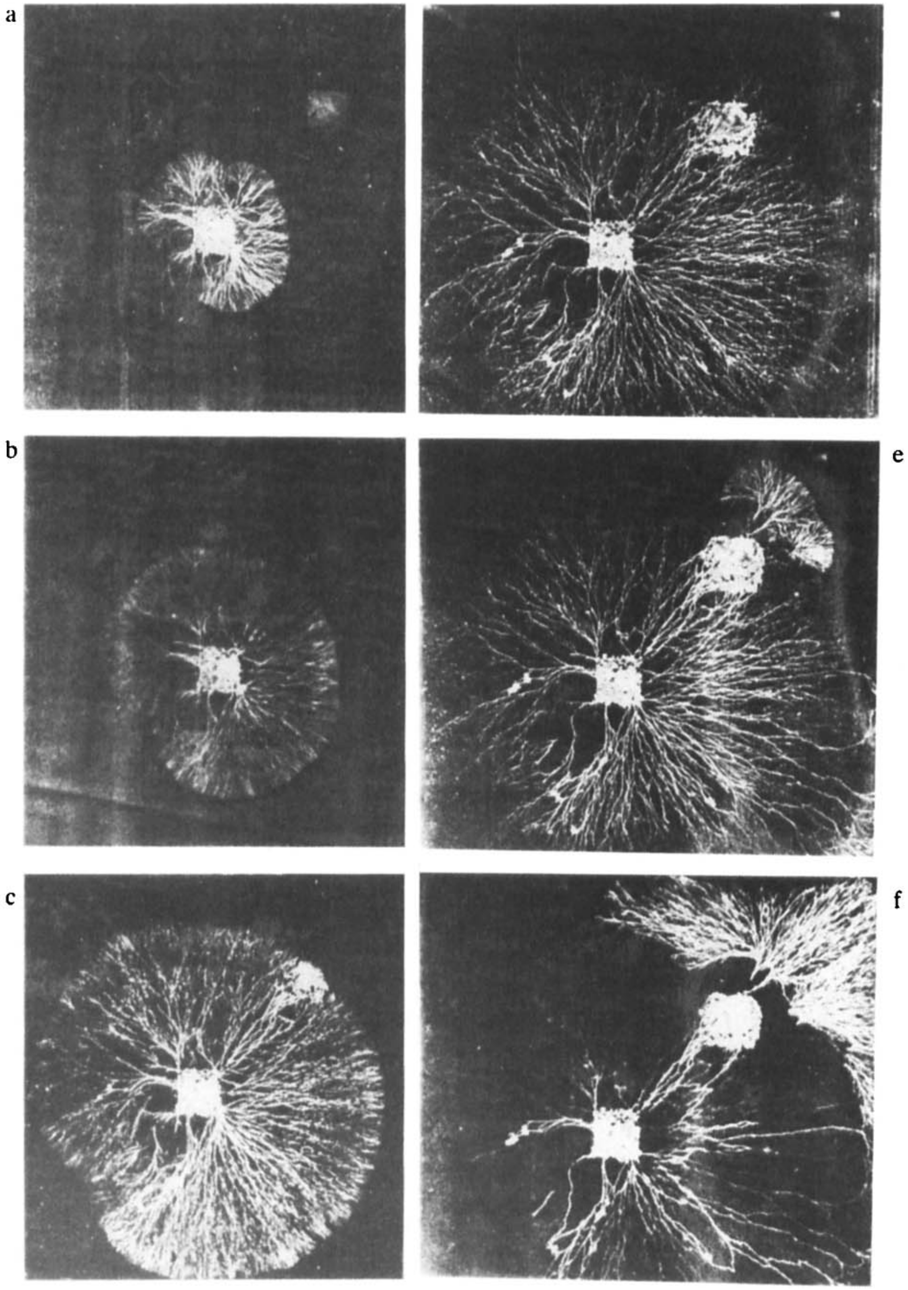
Roots of many species tend to aggregate where resources are abundant in the soil. The aggregation is the result of an increase in the formation and growth of lateral roots in response to local enrichment. The extension growth of the main root axis may be unaffected by the nutrient status of the patches in the soil, suggesting that the soil is continuously searched, while plasticity in lateral root formation is responsible for the exploitation of the resources in those favourable patches that are encountered. Not all species have equal plasticity in root morphology; the roots of some species do not seem able to grow selectively into favourable patches. The results of some studies suggest that more competitive species and species from soils which are relatively rich in nutrients have higher levels of root plasticity than less competitive species and species from poor soils, but conflicting results have been reported. It has been suggested that large unresponsive root systems are better at utilizing short, unpredictable nutrient pulses, such as those which occur in unproductive habitats, than are fast growing roots with high morphological plasticity (see Section VII).

VI. THE FORAGING ACTIVITIES OF FUNGI

Rayner and Franks (1987) have drawn parallels between the foraging behaviour of the mycelia of fungi and the social organization of colonies of ants. Both fungi and ants must mobilize units of structure which search for resources, from a food base upon which they are initially dependent, into new habitat. Parts of the newly explored habitat may lack the resources which are sought. Achievement of the objective of finding essential resources, and making the best use of them, necessitates coordination and cooperation between the parts of the structure which find the resources and the established food base.

There is strong evidence for coordinated foraging activities in fungi, at least in species from stable environments (Dowson *et al.*, 1986, 1988, 1989a,b). Dowson and his co-workers placed wood blocks ("food bases") inoculated with mycelial cord-forming basidiomycetes in plastic dishes filled with sand. One or more sources of nutrition, such as wood blocks, beech leaves or pine cones, were placed in the dishes at some distance from the food base. Both verbal descriptions and photographic evidence are provided of the ability of the mycelia to selectively forage for these sources of nutrition (Fig. 6). Once such a source has been discovered by the radially expanding fungus, the mycelia connecting the food base to it are stimulated to thicken, presumably to enable transport of more materials from the resource to the rest of the fungal body. Many mycelia which were not originally growing towards the resource are seen to reorientate towards it, and those mycelia which are still unsuccessful in discovering sources of nutrition eventually regress. As a result the fungus stops growing radially from its source, showing instead preferential growth towards the resource-rich areas (Fig. 6). The degree of change in growth form was greater when more valuable sources of nutrition were discovered. Regardless of the number of sources of nutrition offered, similar behaviour was always observed (Dowson *et al.*, 1989b), with the fungus redirecting its growth towards newly discovered sources of nutrition and proliferating upon them. The mechanisms which coordinate such foraging activities in fungi are not known.

Fig. 6. Outgrowth pattern of *Hypholoma fasciculare* from a large inoculum and its response to contact with an equal sized bait after (a) 8 days, (b) 20 days, (c) 31 days, showing the regular margin present on contact with the bait, and thickening of connective cords, (d) 51 days, showing irregular morphology at the edge of the mycelium, (e) 68 days, showing outgrowth from the bait and regression of non-connective mycelium, (f) 85 days. From Dowson *et al.* (1986).


a
b
c
e
f

There are marked differences in the growth forms of fungi. Species which are specialized in their choice of substrate exhibit strong rhizomorphic outgrowth, with marked apical dominance, whereas those with less specialized requirements have a more diffuse growth pattern with less apical dominance (Rayner and Franks, 1987). The patterns of expansion growth also differ. Among the fairy ring fungi the species *Clitocybe nebularis* grows in a nutritionally rich habitat, exploiting recently fallen leaf litter. It has a rapid extension rate and a sparse mycelium, it vacates occupied ground rapidly, without exploiting all of the resources on offer, and it is uncompetitive in interactions with other species. Several other woodland litter decomposers can be contrasted with this, particularly *Marasmius wynnei* (Dowson *et al.*, 1989a), which has very dense, slowly-moving mycelia which utilize a high proportion of the resources on offer at any site. It would be very interesting to investigate the extent to which these species differ in their capacity to locate discrete sources of nutrition in their vicinity and the levels of resource extraction they can accomplish in environments with different patch structure.

VII. WHOLE-PLANT COORDINATION OF FORAGING

In our discussion of the foraging activities of shoots and roots we have presented information about the morphological responses of plants and plant parts to differences in resource supply, and the capacity of plants to select favourable habitat patches for the placement of resource-acquiring structures. Many resources acquired locally are transported from the site of acquisition to other locations, so that the benefits of acquisition can appear elsewhere in the structure of the plant. We now discuss the extent to which the morphological responses of the plant to its environment are influenced by the resource status of the whole plant. We also consider whether the level of morphological plasticity expressed locally is influenced by conditions experienced by other parts of the plant located in habitat of different quality. Local patterns of growth could be profoundly affected by transport of resources and growth substances between connected modules. Such integration could alleviate local resource shortage (Pitelka and Ashmun, 1985; Marshall, 1990), and this might enable the morphology of plant parts growing under low resource supply to more closely resemble that of parts growing under high resource supply. We finally discuss resource uptake and integration in clonal plants in patchy habitats in which the distributions of different resources are negatively correlated in space.

A. Effects of Integration on Local Foraging Responses

In Section V we presented evidence showing that local nutrient enrichment of the soil may promote local formation and extension of lateral roots. Local conditions determine *where* lateral root growth is promoted (Drew *et al.*, 1973; Drew and Saker, 1975), but the *magnitude* of the local response depends on the conditions experienced by the rest of the root system. An experiment by Drew (1975) illustrates this well. He subjected roots of barley plants to either a uniform or localized nutrient supply. Part of the root system given a high phosphate supply produced more and longer lateral roots when the rest of the root system was receiving low phosphate rather than high phosphate (see Fig. 4). This suggests that the local morphological response is stronger when phosphate is more limiting to the plant. In addition, lateral root formation under low local phosphate availability was higher when the rest of the root system was given high compared to low phosphate supply (Fig. 4), suggesting that the effects of locally abundant phosphate on root morphology were carried over into adjacent parts of the root system growing under phosphate deficiency. Broadly similar effects were produced when the nitrate and ammonium supply to different sections of the root system were varied (Drew, 1975). However, effects were less clear for nitrate (Drew *et al.*, 1973; see Fig. 4). Similar effects of integration in root systems were observed in fertilization experiments with three *Plantago* species (de Jager and Posno, 1979) and with pea seedlings (Gersani and Sachs, 1992), but not in a similar study with maize (de Jager, 1982). When local nutrient availability allows for rapid root initiation, the root may become the preferred sink for carbohydrates and auxins provided by the shoot, inducing enhanced root development in sections with higher nutrient supply (Gersani and Sachs, 1992). Morphological responses to local water stress may also be affected by integration. For example, Evans (1992) grew the rhizomatous herb *Hydrocotyle bonariensis* under different levels of water availability. Large root systems were produced by ramets in response to water stress, but root systems were much smaller when water-stressed ramets were connected to ramets rooting in wet soil.

The effects of integration on shoot morphology have mostly been investigated in species with plagiotropic shoots. Slade and Hutchings (1987c) grew single stolons of *Glechoma hederacea* clones from resource-poor into resource-rich conditions and *vice versa*. Under unshaded conditions, short stolon internodes were formed irrespective of the conditions experienced by other parts of the stolon. Internodes were longer under shaded conditions, but when stolons grew from unshaded conditions into shade, the first two internodes formed under shade were shorter than the subsequent ones (Fig. 7A). Thus the effects of high photon flux density on stolon morphology were carried over acropetally into adjacent parts of the stolon growing under low photon flux density. The morphology of still more distal regions of the stolon was unaffected by such integration. This observation may be explained by the fact that most translocates from the ramets growing in unshaded conditions are transported into new, higher-order stolons growing from their leaf axils,

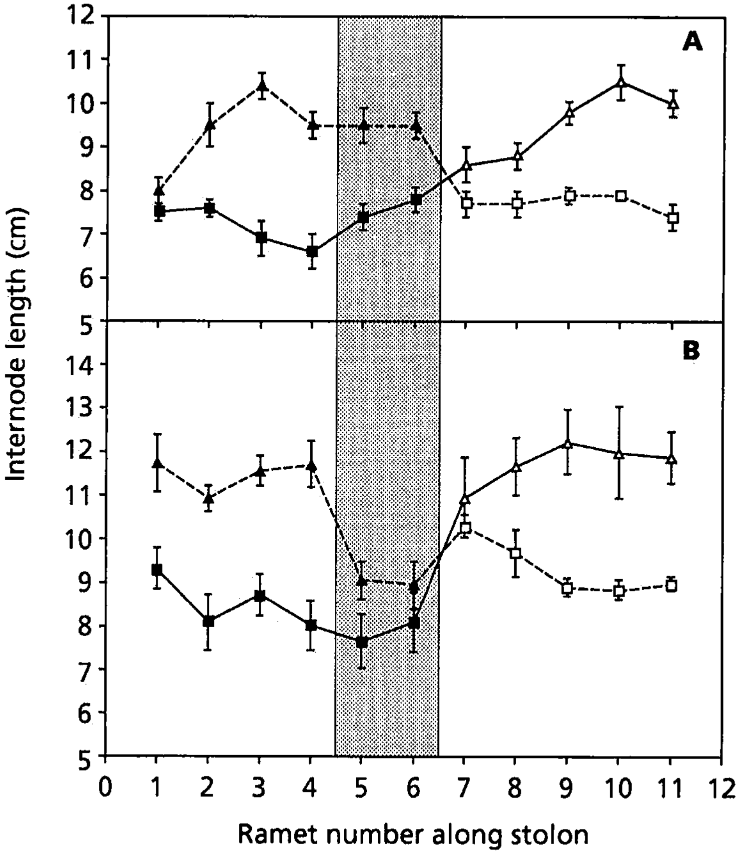


Fig. 7. Mean (± SE) lengths of sequentially produced primary stolon internodes of (A) *Glechoma hederacea* and (B) *Lamiastrum galeobdolon*. In the treatment marked (■–△) clones grew from high light into low light conditions; in the treatment marked (▲–□) they grew from low light into high light conditions. The shaded band in the figure indicates the stolon internodes which were still elongating under "old" light conditions at the time when the stolon apex grew into "new" light conditions. In A, low light was neutral; in B, low light also had a low R/FR ratio. After Slade and Hutchings (1987c) for *G. hederacea* and Dong (1993) for *L. galeobdolon*.

instead of along the original stolon axis (see Price *et al.*, 1992; Price and Hutchings, 1992).

Lamiastrum galeobdolon (like *G. hederacea*, a member of the Labiatae) displayed similar localized morphological responses to light (Dong, 1993) but did not show the same carry-over effect: instead, its internodes *abruptly* increased in length when stolons grew from high light into shade (Fig. 7B). It did exhibit another effect of integration, however. When stolons grew from low into high light conditions, the last two internodes formed under low light were already as short as those formed under high photon flux density (Fig. 7B). These internodes were still elongating when the apex of the stolon penetrated the high light patch. Thus, exposing the apical region of the stolon to high light resulted in significant internode shortening even when older, expanding internodes experienced low light. In the opposite situation, when the apical region was subjected to low light and the expanding internodes to high light, the influence of high light upon morphology prevailed, and short internodes were also formed (Fig. 7B). Dong (1993) speculated that these responses were caused by hormone transport enabling the plant to sense the smallest high light patches in its environment and immediately respond to them. Responses of *L. galeobdolon* petiole lengths to light supply were also investigated. Petiole extension by ramets under low photon flux density was less when they were connected to ramets growing under high photon flux density than when the entire clone was growing under low light conditions. This effect was not seen when only the apical region of the stolon was in high light.

Integration had no effect on the length of internodes formed by the rhizomatous species *Hydrocotyle bonariensis* under lower photon flux density (Evans, 1992). However, the tendency of lateral rhizome buds to grow out under low resource levels was higher when the rhizome was connected to a sibling rhizome growing under high resource levels than when the connection was severed. The longer petioles and larger leaf blades produced under shaded conditions *increased* further in size when connected to a rhizome branch that was growing under unshaded conditions. Evans (1992) suggested that integration may thus facilitate the projection of leaf blades into the high light zone of the canopy. It is noteworthy that *L. galeobdolon*, in which the effect of integration on petiole growth was the opposite of this, is a species of woodlands, unlike *H. bonariensis*. In woodlands it may not be possible for a species with plagiotropic shoots to increase its access to light by employing morphological responses which raise the positions of leaves. Like *H. bonariensis*, *Trifolium repens* ramets in a grass sward produced longer petioles and more secondary stolons when connected to sibling ramets growing in bare soil than they did when the sibling ramets were also growing in competition with grasses (Turkington and Klein, 1991). Stolon internodes of *T. repens* also increased in length when connected to ramets growing under more favourable conditions.

In many plant species, structural branches or ramets have a high degree of autonomy (Watson and Casper, 1984; Sprugel *et al.*, 1991; Price *et al.*, 1992). This occurs when the sectorial arrangement of vascular strands in orthostichies results in an absence of vascular connections between branches or ramets, preventing exchange of carbohydrates and other resources between them. These semi- to fully autonomous structures have been named integrated physiological units (IPUs). Necessarily, the morphology of IPUs will be a pure response to local conditions which is unaffected by translocation of resources from other IPUs. Thus, in a patchy habitat, despite their being physically connected, the morphology of each IPU of a single plant could be strikingly different. For example, such sectoriality in *Glechoma hederacea* clones precludes resource transport between the sibling stolons that originate from a single ramet (Price *et al.*, 1992), and consequently each stolon, and the ramets it bears, responds independently to its local environment (Slade and Hutchings, 1987a). It has been suggested that an autonomous, non-integrated behaviour of structural branches or ramets may enhance foraging efficiency by increasing the growth of those resource-acquiring structures which are in the most favourable patches of habitat (de Kroon and Schieving, 1990; Sprugel *et al.*, 1991). In time this will increase the proportion of resource-acquiring structures occupying favourable patches. In contrast, integration between branches occupying habitat of differing quality would result in more uniform growth of all parts of the plant; the branch in poor quality habitat would be sustained, and its growth increased by translocation from the branch in good quality habitat. Provision of support could, however, limit the growth of the branch in good quality habitat.

B. Division of Labour

Most natural habitats are spatially and temporally patchy in the provision of resources. It is possible that few microsites provide all essential resources in adequate quantities. The availability of different essential resources may also be negatively correlated in space (Friedman and Alpert, 1991). For example, a high local availability of nutrients may lead to a local concentration of biomass of tall species, producing a low availability of light at ground level. When the spatial supply of different resources is negatively correlated there may be benefits in a "division of labour" in resource capture between different parts of the plant (Callaghan, 1988). The species most likely to exhibit such behaviour are clonal plants with plagiotropic stems.

An example is seen in the clonal graminoid *Carex bigelowii*, which has long-lived ramets interconnected by persistent rhizomes (Jónsdóttir and Callaghan, 1988, 1990). Different ramet generations undertake different tasks of resource acquisition. The youngest ramets are photosynthetic and they provide carbohydrates which support the forward growth of rhizomes and new ramets, and sustain the root systems of several generations of older ramets. The older generations of ramets are leafless. The combined root systems of these old generations of ramets exploit a large volume of soil for nutrients and water, and a proportion of these resources is transported to the growing points of the rhizome system, thus supplementing the limited capacity of the youngest, photosynthetic generations of ramets to acquire soil-based resources. A similar division of labour may occur in the tundra clubmoss *Lycopodium annotinum* (Headley *et al.*, 1988) and the forest understorey perennial *Podophyllum peltatum* (de Kroon *et al.*, 1991; Landa *et al.*, 1992). However, only a small percentage of the total nutrient uptake by the older roots is transported acropetally towards the growing tips (Headley *et al.*, 1988; Jónsdóttir and Callaghan, 1990), and the importance of this transport for the growth and survival of younger parts has yet to be established. The results of rhizome severing studies do not provide a general answer: severing old rhizome segments significantly decreased shoot survival and new rhizome growth in *C. bigelowii* (Jónsdóttir and Callaghan, 1988), but in *P. peltatum* new rhizome growth was unaffected, at least in the short term (de Kroon *et al.*, 1991).

Data on the stoloniferous herb *Fragaria chiloensis* suggest that water and photosynthates can simultaneously move in opposite directions within the same stolon. Connected ramets can therefore exchange different resources and rectify local deficiencies in a heterogeneous habitat. Alpert and Mooney (1986) showed that if a ramet growing under low light levels, but with ample water supply, was connected to a ramet under water stress but with sufficient light, both grew successfully, although isolated ramets could not survive under each of these conditions. Reciprocal exchange of water and carbon may thus enable the plant to grow in a patchy environment which would otherwise be uninhabitable. A subsequent study (Friedman and Alpert, 1991) purported to show similar effects of reciprocal translocation of carbohydrates and nitrogen in *F. chiloensis*. However, no evidence was obtained to show that nitrogen was actually translocated between sibling ramets under the experimental conditions applied. In an experiment with two species of *Potentilla*, plants reached a higher total biomass under conditions in which either the mother ramet was growing under shaded and the daughter stolon under unshaded conditions, or *vice versa*, as compared to uniform shaded or unshaded conditions (J. Stuefer, H.J. During and H. de Kroon, 1993, unpublished). There were indications that ramets under unshaded conditions experienced water stress, and Stuefer *et al.* suggested that the higher biomass obtained under heterogeneous conditions was the result of reciprocal translocation of water and carbohydrates between mother and daughter parts.

Physiological integration, and a division of labour between ramets, may also provide clonal plants with the ability to exploit below-ground resources in a resource-rich patch of habitat, while avoiding the above-ground competition that could result from the biomass produced with these resources. Birch and Hutchings (1994) have shown that *Glechoma hederacea* ramets rooted vigorously in nutrient-rich patches surrounded by nutrient-poor sand, and that this resulted in a high ramet production by the clone (Fig. 8). The majority of these ramets were placed *beyond* the nutrient-rich patch and they occupied a wide area of ground. As a result, the risk of extreme ramet density was alleviated and severe intraclonal competition for light was avoided.

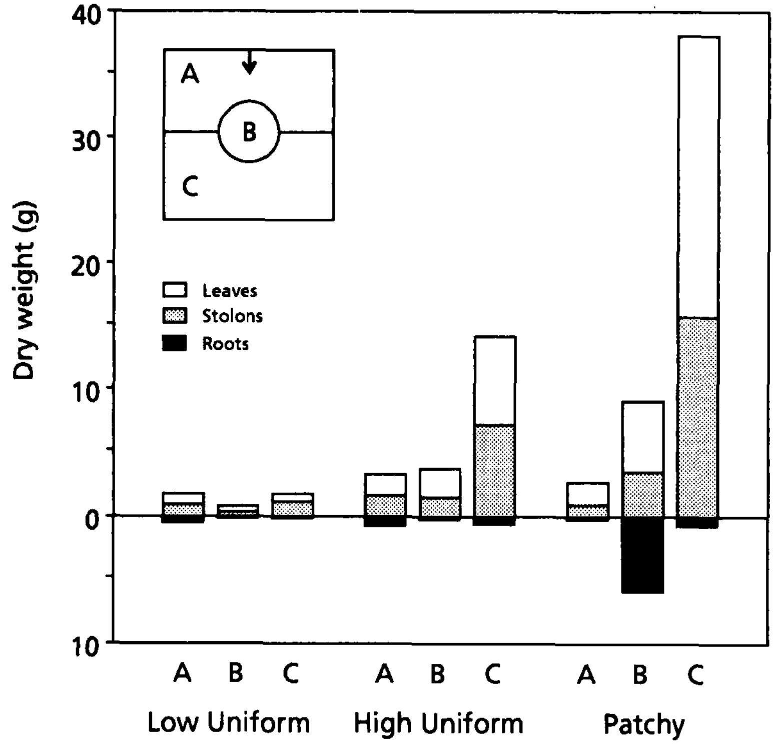


Fig. 8. Division of labour in the clonal herb *Glechoma hederacea*. Clones were grown in square boxes in one of three artificial soil environments made by distributing washed sand and potting compost throughout the box in different ways. In the "High Uniform" treatment, potting compost was mixed evenly with sand throughout the box. The "Patchy" treatment provided a heterogeneous soil environment made by using the same quantity of potting compost as in High Uniform, but concentrating half of it in a 30 cm circle in the centre of each box (11% of the box area). In the treatment "Low Uniform", compost was distributed homogeneously, as in the High Uniform treatment, but the total quantity of potting compost was halved. At harvest the biomass of the plants in each of three compartments was determined: (A) the near half of the flat with parts of the clone that developed prior to entering the patch, (B) the central circle and (C) the far half of the flat predominantly containing stolons with basipetal connections to ramets growing in the central circle. In the case of the patchy resource distribution, the majority of the roots developed in the central nutrient-rich circle while most of the above-ground biomass was formed outside the circle. After Birch and Hutchings (1993, unpublished).

C. Conclusions

Data suggest that locally favourable conditions may intensify the local placement of resource-acquiring structures, irrespective of the conditions experienced by other parts of the plant. Total resource demand by a plant does not affect the *location* of placement, but may affect the *magnitude* of the morphological response to environmental conditions. This has been demonstrated convincingly for root systems which branch more vigorously in nutrient-rich patches when nutrients are more limiting to the plant. We are not aware of any studies showing similar responses for shoot systems. When clones with interconnected ramets are subjected to heterogeneous conditions, different studies have shown that local responses of bud activation to patch quality are damped, responses of shoot height increment are either damped or intensified, and stolon internode length responses are mostly unaffected by integration. Thus, resources received by part of a plant through intraclonal transport may alter the morphology of the recipient part from the pattern which would be produced purely in response to its local resource supply. Such effects of integration have been interpreted in terms of foraging efficiency. Patches of habitat may not be simply classifiable as "favourable" to a particular degree dependent on the availability of a single resource. Each essential resource may vary independently in time and space, so that all parts of the habitat may be favourable for some resources but unfavourable for others. When the spatial supply of different resources is negatively correlated, ramets of clonal species may divide the tasks of acquiring different resources in a manner which reflects the local availability of each resource. In such situations resource sharing between ramets is beneficial to the growth of the clone.

VIII. PHYSIOLOGICAL PLASTICITY AS AN ALTERNATIVE TO MORPHOLOGICAL PLASTICITY FOR RESOURCE ACQUISITION

Foraging responses by a plant in a patchy environment may enhance resource acquisition by placing more leaves and roots in patches of the habitat with higher concentrations of resources. However, total resource gain depends not only upon the effective location of leaves and roots in such patches but also on the rate of resource uptake by those leaves and roots. Variation is possible in the rate of acquisition of essential resources as the level of resource availability changes, because of physiological plasticity.

Marked physiological plasticity is predicted to be a particularly valuable attribute in conditions in which resources become available in the form of short, unpredictable pulses above a low background level (e.g. Grime *et al.*, 1986; Hutchings, 1988). This is because the pulses may be too brief and too unpredictable in location to enable them to be exploited sufficiently fast by morphological responses. In such situations physiological plasticity may serve either as an adjunct to, or as a more valuable asset than, morphological plasticity for resource acquisition.

In this section we discuss resource uptake under low levels of resource availability, and the ability of plants to rapidly increase their uptake rates when resource levels increase. We subsequently review what is known about plasticity in nutrient uptake rates in response to nutrient pulses, and plasticity in carbon assimilation in response to sunflecks. Special attention is paid to the levels of physiological plasticity exhibited by species from habitats with differing levels of resource supply, and the extent to which whole plant growth may profit from plasticity in resource uptake rates.

A. Acquisition of Nutrients

Under conditions of high nutrient availability, species from infertile habitats display lower nutrient uptake rates than species from more fertile habitats (e.g. Bradshaw *et al.*, 1964; Chapin, 1980; Chapin *et al.*, 1982; Campbell and Grime, 1989; Garnier *et al.*, 1989; Kachi and Rorison, 1990; Poorter *et al.*, 1991). However, their absorption rates vary less than those of species from fertile habitats over a given range of nutrient concentrations, and thus, when nutrients are scarce, the nutrient uptake rates of species from infertile habitats can equal or even exceed those of species from fertile habitats, even though these rates are low. In general, nutrient uptake rates are greater when the nutrient demand of the plant is higher (Robinson, 1989), and it has been suggested that the magnitude of the uptake rate at a given level of supply is negatively related to the internal nutrient concentration of the plant (de Jager, 1984; Burns, 1991).

In habitats with inherently infertile soils, such as tundra and chalk grassland, a large proportion of the nutrients annually available to plants may be provided in short, unpredictably occurring flushes (see Crick and Grime, 1987; Campbell and Grime, 1989; Jonasson and Chapin, 1991). Physiological plasticity allowing rapid changes in the capacity of roots to absorb nutrients may ensure that these flushes are captured before they can be exploited by the microbial community in the soil. Most mobile nutrients which are not captured by higher plants are absorbed by microorganisms within a few days of release into the soil (Campbell and Grime, 1989; Jonasson and Chapin, 1991).

An elegant illustration of the ability of some plant species to respond rapidly to an unpredictable flush of nutrients is provided by the work of Jackson *et al.* (1990) on three species which grow in phosphate-poor soils in cold desert habitat. The soil on one side of well-established plants was supplied with a solution containing phosphate, while the soil on the other side was given an equal volume of distilled water. Roots were extracted from the sectors treated in these different ways at various times after treatment. For all three species, those parts of the root system extracted from the phosphate-enriched soil showed significant increases in the rate of phosphate uptake per gram of root compared with roots from the soil watered with distilled water.

Two species of bunchgrasses showed this effect within 3 days of treatment. Mean rates of phosphate uptake increased by up to 80% in roots from the enriched patches, with the largest increases being seen when the external phosphate concentration was highest. Later experiments (Jackson and Caldwell, 1991; Caldwell *et al.*, 1991a) confirmed these results (see Fig. 5). Enrichment of soil by nitrogen appeared to significantly increase the uptake of nitrogen and potassium, while phosphate enrichment increased the uptake of phosphate. One of the treated species, *Pseudoroegneria spicata*, showed no increased root development following soil enrichment (Jackson and Caldwell, 1989; Caldwell *et al.*, 1991b) (see Fig. 5). Thus, its response to a pulse of nutrients was entirely physiological. In this short-term experiment (3–5 weeks), the change in uptake kinetics achieved by means of physiological plasticity in *P. spicata* was more effective in acquiring phosphate from enriched as opposed to control patches than that of *A. desertorum*, which combined *both* morphological and physiological responses to increased phosphate supply. Finally, it is important to realize that even without a change in uptake kinetics, resource acquisition is markedly increased when soil resource concentrations are elevated (Caldwell *et al.*, 1992).

A higher degree of physiological plasticity may result in higher growth rates under a regime of ephemeral nutrient patches. Poorter and Lambers (1986) grew *Plantago major* in a growth chamber under continuous or fluctuating nutrient supply. The same total amount of nutrients was applied in pulses of different duration. Relative growth rate of the plants was inversely related to pulse length, but with decreasing pulse duration, a highly plastic inbred line maintained higher growth rates than a marginally plastic inbred line. The magnitude of the difference was greater when plants of the two lines were grown in competition.

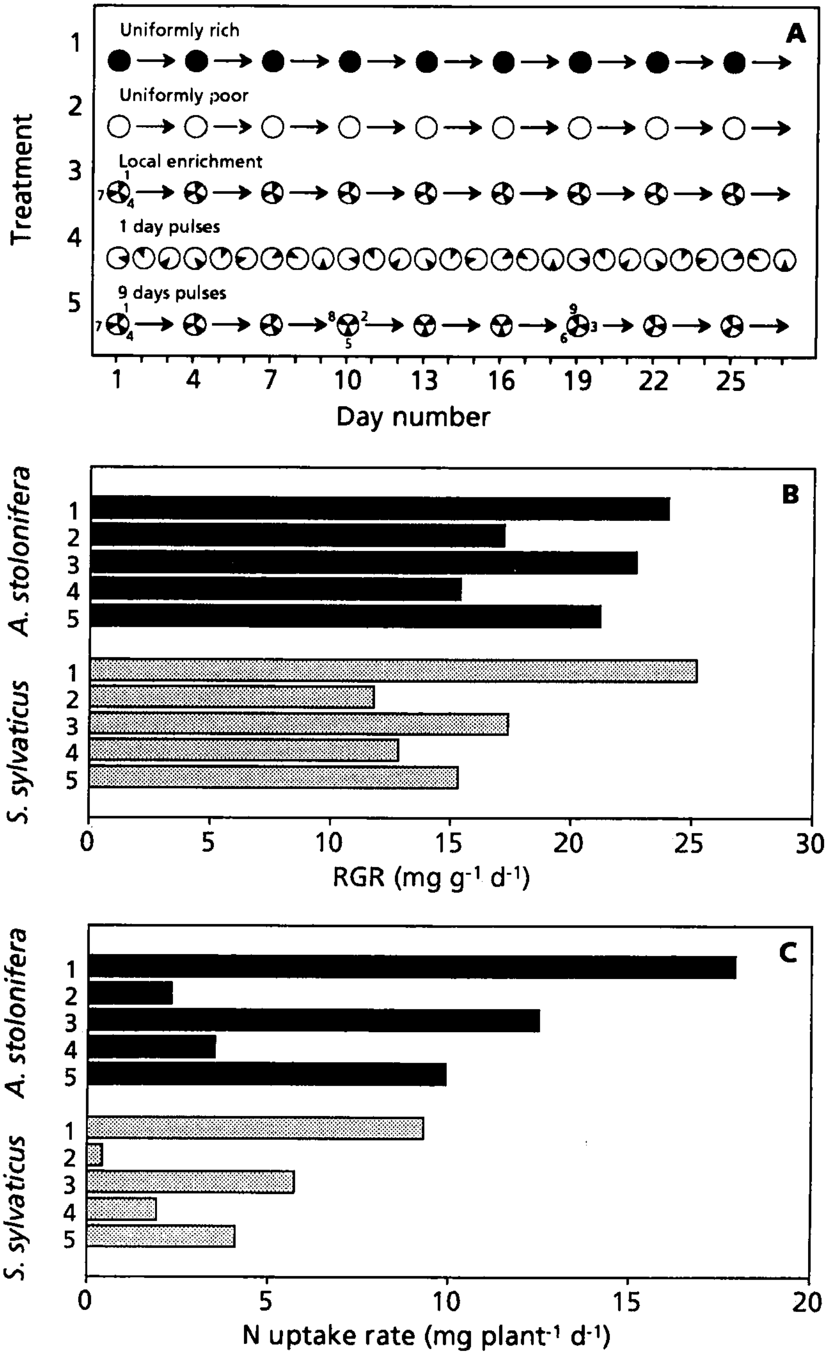
A number of studies have investigated whether slow-growing species from poor soils are better at utilizing nutrient pulses than fast-growing species from richer soils. De Jager and Posno (1979) supplied *Plantago* seedlings after a period of phosphate depletion with a full-strength nutrient solution, applied either to the entire root system or to a small part of it. Phosphate uptake rate ($\mathrm{mmol\,g^{-1}\,d^{-1}}$) of *P. media*, a species from relatively nutrient-poor habitats, increased more strongly than that of *P. major*, a species of more fertile habitats, in response to a localized supply of phosphate. However, Kachi and Rorison (1990) found that *Holcus lanatus*, a grass species from nutrient-rich habitats, had similar nitrogen uptake rates to *Festuca rubra*, a grass species from nutrient-poor habitats, when their roots were subjected to high nutrient levels after a period of nutrient depletion.

Campbell and Grime (1989) compared the nutrient uptake characteristics of *Festuca ovina* with those of *Arrhenatherum elatius*, another grass species from fertile habitats. Both were grown hydroponically in conditions in which periods of low nutrient supply were interspersed with pulses during which nutrient-rich solutions were applied. Pulse duration varied from 80 seconds to 6 days, with a single pulse applied at the midpoint of each 6-day period throughout the experiment. Nitrogen absorption rates per unit of root weight were greater in *A. elatius* when long nutrient pulses were supplied, but greater in *F. ovina* for all pulse durations shorter than 10 hours. Under these short pulse durations *F. ovina* maintained higher root:shoot ratios and more viable leaf tissue than *A. elatius*. As a result, under all pulse lengths shorter than 10 hours, nitrogen capture by plants of the two species was similar, despite the far greater size of *A. elatius*, and *F. ovina* had higher relative growth rates. *A. elatius* grew faster at longer pulse lengths. However, as the concentration of the nutrient solution used was the same in all pulse treatments in this experiment, total nutrient supply to the plants increased with increasing pulse duration. Thus, the results must be interpreted with caution, because responses to pulse duration cannot be separated from responses to total nutrient supply.

Crick and Grime (1987) grew *Scirpus sylvaticus*, a species of nutrient-poor habitats, and *Agrostis stolonifera*, a species of nutrient-rich habitats, in an apparatus enabling given fractions of the root system to be supplied with high or low nutrient solutions for specified lengths of time. In one treatment (no. 4; see Fig. 9A) nutrients were supplied in short (1-day) pulses to sectors of the root system selected virtually at random, i.e. the timing and location of the nutrient pulses were effectively unpredictable to the plant. In another treatment (no. 2), the whole root system received a continuous supply of low nutrient solution. Relative growth rates of both species were altered little by imposition of either of these treatments, but both species achieved a greater rate of nitrogen uptake when provided with unpredictable pulses of nutrients (Fig. 9). However, the proportional increase in nitrogen uptake rate between the pulse treatment and the continuously low nutrient treatment was considerably greater (nearly fivefold) for *S. sylvaticus*, the species from nutrient-poor habitats, than for *A. stolonifera*, in which it was only about 50%. We would conclude from this analysis that *S. sylvaticus* is more effective than *A. stolonifera* in capturing ephemeral nutrient pulses above a low background level.

However, in two further treatments, the same quantity of nutrients as provided in the pulse treatment was supplied either in a more stable configur-

Fig. 9. Relative growth rate (RGR) (B) and nitrogen uptake rate per plant (C) in an experiment in which *Agrostis stolonifera* and *Scirpus sylvaticus* were grown in a root growth arena that allowed a separate control of nutrient supply in each of nine root sectors. The roots were subjected to five patterns of nutrient supply differing in spatial and temporal configuration as depicted in A. See text for further explanation. Recalculated from Crick and Grime (1987).


A
Treatment
1
Uniformly rich
2
Uniformly poor
3
Local enrichment
4
1 day pulses
5
9 days pulses
1
2
3
4
5
6
7
8
9
1
4
7
10
13
16
19
22
25
Day number
B
A. stolonifera
S. sylvaticus
1
2
3
4
5
0
5
10
15
20
25
30
RGR (mg g-1 d-1)
C
A. stolonifera
S. sylvaticus
1
2
3
4
5
0
5
10
15
20
N uptake rate (mg plant-1 d-1)

ation (9-day pulses; treatment no. 5) or in a completely stable configuration (treatment no. 3). The relative growth rates and nitrogen uptake rates of both species were greater in both of these treatments than in the 1-day pulse treatment (Fig. 9). The proportional reduction in uptake rate in the random pulse treatment (no. 4) compared with the stable configuration treatment (no. 3) was approximately the same in both species (72% in *A. stolonifera*, 67% in *S. sylvaticus*; see Fig. 9C). If the nutrient uptake efficiencies under random pulse supply (no. 4) are calculated as a percentage of that achieved when the same nutrient supply is provided in the more stable configuration of treatment no. 5, the two species still appear to show little difference; the value for *A. stolonifera* was 35%, while that for *S. sylvaticus* was 46%. This analysis is far less convincing in showing that the species from infertile habitats was more efficient in acquiring brief, unpredictable pulses of nutrients. For *S. sylvaticus*, a relatively large root mass (approximately twice as large as the root mass of *A. stolonifera*; Crick and Grime, 1987, Fig. 2) was important for the acquisition of short nutrient pulses. *A. stolonifera* accomplished nutrient acquisition from these short pulses—as in all other treatments—by having higher nutrient absorption rates (see Fig. 9).

The maintenance of a large long-lived mass of roots, and an ability to commence absorption of nutrients quickly when conditions permit, despite long periods of low nutrient availability, seem to be of great importance in enabling species to acquire nutrient pulses of short duration (Crick and Grime, 1987; Campbell and Grime, 1989; Kachi and Rorison, 1990). However, the available data do not unambiguously show that species from nutrient-poor habitats are better capable of taking up nutrients supplied in the form of ephemeral pulses than species from nutrient-rich habitats.

B. Acquisition of Carbon

Björkman (1981) succinctly lists the differences in photosynthetic characteristics between shade-tolerant ("shade") and shade-intolerant ("sun") species. Leaves of obligatory shade species typically have low dark respiration rates resulting in low light compensation points which allow them to maintain higher rates of photosynthesis under shaded conditions than sun species. At higher photon flux densities the inherently low contents of photosynthetic enzymes such as Rubisco in leaves of shade plants result in inherently low maximum rates of photosynthesis compared to sun plants. Moreover, high photon flux densities may cause damage to the photosynthetic equipment of shade plants through photoinhibition. Sun and shade species also differ in a number of leaf morphological characteristics, with shade plants developing larger leaf areas per unit of plant weight (leaf area ratios) and larger leaf areas per unit weight of leaf (specific leaf areas) in response to shading than sun plants. Shade-intolerant species may acclimate to shade and develop physiological and morphological characteristics similar to those of shade species. However, their responses to photon flux density are not of a magnitude sufficient to match the efficiency of light use in shade plants.

In tropical forests, and in temperate deciduous forest during the summer, sunflecks typically contribute 40–50% of the total daily photon flux density (PFD) (Chazdon, 1988; Chazdon and Pearcy, 1991), and on clear days this value can rise to 90%. Sunflecks may strike leaves for a very small fraction of the day. In a Mexican rain forest the total duration of sunflecks ranged from 0 to 42 minutes per day at different points on the forest floor (Chazdon, 1988). Fifty-six per cent of the sunflecks were less than 4 seconds, and 90% less than 32 seconds in duration. While the exact time at which sunflecks will occur is unpredictable, their temporal pattern through the day is far from random. In tropical forest in north-eastern Australia, 70% of sunflecks occurred within one minute of the preceding sunfleck and only 5% were preceded by low light periods longer than an hour (Pearcy, 1988). Fewer sunflecks occur in the morning and evening when the sun is low in the sky, because of the longer path length of its rays through foliage. Peak photon flux densities during sunflecks are relatively low and rarely amount to values reached outside the forest.

Sunflecks are most important for the growth of plants in forest understoreys. For example, Pearcy (1983) found that the relative growth rate of tree seedlings in Hawaiian tropical rain forest was linearly related to sunfleck activity (but see Pfitsch and Pearcy, 1992). On clear days 40–60% of the daily CO_2 uptake of plants in forest understoreys may take place during sunflecks (e.g. Pfitsch and Pearcy, 1989a), and it has been shown that net carbon gain during sunflecks of a given PFD can be substantially greater than predicted from knowing the steady-state rate of photosynthesis of a species at the same PFD (e.g. Chazdon and Pearcy, 1986a; Pons and Pearcy, 1992). Chazdon (1988), Pearcy (1990) and Chazdon and Pearcy (1991) have succinctly reviewed the mechanisms responsible for this efficient use of light pulses. The efficiency appears to be due to the maintenance of high levels of photosynthetic induction during a sequence of sunflecks, combined with substantial post-illumination CO_2 fixation. Here we briefly summarize what is known about these processes.

Leaves exposed to high radiation levels after a long period of low light require a light-priming induction period of up to 60 minutes before a steady-state photosynthetic rate is reached. During the first 6–10 minutes of exposure to high light, the photosynthetic rate is limited primarily by biochemical processes, in particular by the activity of the carboxylating enzyme Rubisco (Chazdon and Pearcy, 1986a; Pfitsch and Pearcy, 1989b; Pons *et al.*, 1992). Stomatal conductance may become a limiting factor later on during exposure to high light. To our knowledge only one species (the fern *Poly-*

podium virginianum) is known to lack a measurable induction period in the field (Gildner and Larson, 1992).

It has been shown that the degree of induction accumulates during a sequence of rapid consecutive sunflecks. Over a sequence of five 30- or 60-second sunflecks, each separated by 2 minutes of low light, the induction state of leaves of two Australian rain-forest species increased two to three times, and rate of induction during these brief sunflecks matched that achieved under constant illumination (Chazdon and Pearcy, 1986a). The shade-tolerant species *Alocasia macrorrhiza* reached higher levels of induction during the first lightfleck than the shade-intolerant *Toona australis*, and maintained this higher level of induction throughout a sequence of lightflecks. In soybean a constant induction state could be achieved by providing 1-second lightflecks; the degree of induction reached was greater when the lightflecks were provided at a higher frequency (Pons *et al.*, 1992). Thus, the clustered temporal pattern of sunflecks in forests may be of great importance for carbon gain as leaves are partially induced by each preceding sunfleck and can therefore use some of the available light from nearly all sunflecks occurring during the day. Tinoco-Ojanguren and Pearcy (1992) showed that the shade-tolerant Mexican rain-forest species *Piper aequale* was better able to make use of such a sequence of sunflecks than the shade-intolerant *Piper auritum* because shade-acclimated plants of *P. aequale* increased more rapidly in stomatal conductance than *P. auritum* in response to sunflecks.

Induction is lost when leaves are subjected to continuous shade (e.g. Pons *et al.*, 1992). Chazdon and Pearcy (1986a) found that completely induced leaves of *A. macrorrhiza* took over an hour in continuous low light conditions to return to a completely uninduced state, but the loss of induction was far more rapid for *T. australis*. Similarly, the stomatal conductance of *P. aequale* decreased more slowly after a sunfleck than that of *P. auritum* (Tinoco-Ojanguren and Pearcy, 1992). This suggests that shade-tolerant species lose induction less rapidly than shade-intolerant species. However, *Adenocaulon bicolor*, a shade-tolerant herb from Californian redwood forests, also rapidly lost induction under shade (Pfitsch and Pearcy, 1989b), which limited its capacity to use sunflecks interspersed by periods of shade longer than 1–2 minutes.

The efficiency of sunfleck use is increased substantially by post-illumination CO_2 fixation (Chazdon, 1988; Pearcy, 1990). For example, when *A. macrorrhiza* is given a 5-second sunfleck, CO_2 assimilation during and after the sunfleck can give 60% greater net carbon gain than would occur during 5 seconds of steady-state photosynthesis at the same photon flux density (Sharkey *et al.*, 1986). This increase appears to be due to a build-up of pools of triose phosphates—photosynthetic intermediates that are synthesized immediately after the sunfleck. Sun-grown plants do not have the large pool of triose phosphates following exposure to a sunfleck, and therefore cannot match the benefit gained from short sunflecks by shade-grown plants (Sharkey *et al.*, 1986). Chazdon and Pearcy (1986b) found that at all sunfleck durations the shade-tolerant *A. macrorrhiza* had both a higher photosynthetic efficiency and a greater net carbon gain than the shade-intolerant *T. australis*. It is unclear whether this was due to maintenance of a higher state of photosynthetic induction during a sequence of sunflecks, to a higher level of post-illumination CO_2 fixation, or both.

Post-illumination CO_2 fixation may compensate for both low photosynthesis under the relatively low peak PFDs of most of the sunflecks in forest understoreys, and for the typically low state of induction of the leaves of plants in such habitats. This compensation is most apparent for short sunflecks (less than approximately 40 seconds); photosynthetic efficiency rapidly decreases with increasing sunfleck duration, for a number of reasons. For example, leaves of C_3 plants release a burst of CO_2 upon darkening as a result of respiring a residual pool of photorespiratory metabolites, but no such burst is apparent after lightflecks shorter than 20 seconds (Pearcy, 1990). In addition, if the PFD of a sunfleck is very high, the efficiency with which it can be used may be reduced because of photoinhibition, particularly in those shade-tolerant species in which photosynthesis is saturated at low light levels (Chazdon, 1988). This will be especially important during long (more than about 10 minutes) sunflecks, but there is no evidence to date to show that photoinhibition significantly limits carbon gain under natural regimes of short sunflecks (Pearcy, 1990). High photon flux densities may also limit photosynthesis through thermal damage and water stress resulting in stomatal closure, but again such effects will only become apparent during extended sunfleck duration (Chazdon, 1988; Pearcy, 1990; but see Pfitsch and Pearcy, 1992).

It is of interest to consider whether shade-tolerant species can grow faster than shade-intolerant species in a sunfleck-dominated light regime. Rincon and Grime (1989) grew bryophyte species from open and shaded habitats under a number of artificial light regimes. In addition to uniform high and low light, plants were exposed to regimes of either low light with lightflecks provided in a spatially and temporally stable configuration, or spatially unpredictable lightflecks of 20 minutes' duration. Four species from open habitats grew equally well when the same total amount of light was provided as either stable patches or as unpredictable lightflecks, but one of the two species from shaded habitats (*Thamnobryum alopecurum*) grew significantly faster in the unpredictable lightfleck regime than in the stable lightfleck regime. This was also the only species with a significantly higher relative growth rate under unpredictable lightflecks than under uniformly low light. These results suggest that at least one shade-tolerant species grows faster than shade-intolerant species under a temporally unstable lightfleck regime. However, it is unclear whether these bryophytes would respond similarly in a forest understorey habitat in which most of the sunflecks are likely to be much shorter than those applied by Rincon and Grime (1989), because, as discussed earlier, lightfleck photosynthesis is most efficient when the pulses of light occur in clusters.

We conclude that the photosynthetic machinery is well equipped to utilize brief sunflecks that are clustered in time. Such a temporal pattern of sunflecks is typical in many forest understorey habitats. There appears to be much variation in photosynthetic characteristics between species. Although some data suggest that shade-tolerant species can use sunflecks more efficiently than shade-intolerant species, the evidence is inconsistent.

C. Conclusions

In many habitats, the usual level of supply of resources is low. Most resources become available in the form of ephemeral pulses which are unpredictable in time and space. Plants possess mechanisms for efficient acquisition of the resources in such pulses. Nutrient uptake capacity of roots rapidly increases when they are exposed to high nutrient levels following periods of nutrient scarcity, and levels of photosynthesis immediately increase in response to sunflecks interrupting periods of low light. These responses are most effective in terms of the amounts of resources acquired and the growth that is realized with them. A number of studies have investigated whether species from habitats characterized by transient resource pulses are able to utilize such brief pulses more effectively than species from habitats in which resource availability is usually higher and more stable. Support for this hypothesis is equivocal, but few comparative studies have been carried out to date, and few species have been investigated. Levels of physiological plasticity are not always higher in species from habitats in which resource supply is ephemeral; the capacity to maintain viable resource-acquiring structures during periods of resource shortage may be at least as important as physiological plasticity for the capture of temporally unpredictable resource pulses.

IX. GENERAL TRENDS IN THE FORAGING ACTIVITIES OF PLANTS AND THEIR INTERPRETATION

In this review we have explored and documented the foraging behaviour of plants, and concentrates on the ability of plants to actively promote the exploitation of patches of habitat with high levels of resource availability. In this section we present a summary of the hypotheses about foraging behaviour which have been proposed in the literature. Secondly, we survey the patterns which have emerged. Thirdly, we evaluate the extent to which the hypotheses are supported by the patterns. The section is concluded with a list of questions in need of solutions.

A. Hypotheses

An essential consequence of the modular construction of plants is that leaves and root tips (resource-acquiring structures, or "feeding sites") are located at the ends of branches ("spacers") which project them into habitat space (Bell, 1984). The morphology of shoots and roots can be described using a few simple parameters such as spacer length (the distance between consecutive potential branching points), the branching propensity and the branching angle. It has been hypothesized, implicitly more than explicitly, that the heterogeneous distribution of resources in most habitats has acted as one of the major selective forces upon the evolution of morphological plasticity (e.g. Harper, 1985; Hutchings, 1988; Schmid, 1990; Sutherland, 1990; Oborny, 1991). According to this view, morphological plasticity has evolved in such a way as to project resource-acquiring structures into the more favourable patches within the environment and to promote the avoidance or vacation of habitat patches of low quality (Cook, 1983; Hutchings and Bradbury, 1986; Sutherland and Stillman, 1988). Such behaviour is expected to increase resource acquisition from the habitat and thus to enhance plant fitness. Analogous organs, such as orthotropic stems, plagiotropic stems and root branches, have been subjected to similar environmental constraints and therefore will have developed convergent patterns of morphological plasticity (Grime *et al.*, 1986; Hutchings, 1988). It is thus predicted that (i) shaded orthotropic shoots will produce long unbranched stems which effectively grow towards the high light zone at the top of a vegetation canopy (Grime, 1966; Lovell and Lovell, 1985), (ii) clonal plants with plagiotropic stems search horizontal space and place ramets non-randomly within their environment by shortening their spacers and increasing their branching intensity when favourable microhabitats are encountered (Slade and Hutchings, 1987a,b; Hutchings and Slade, 1988; Hutchings and Mogie, 1990), (iii) long root axes search the soil volume and when they grow into a patch of high resource supply, lateral root formation is increased and the resources are exploited (Drew *et al.*, 1973; Fitter, 1991). All of these plastic modifications are expected to be local responses to patch quality. They should ideally be independent of the conditions experienced by the rest of the plant, as widespread integration may decrease foraging efficiency (de Kroon and Schieving, 1990).

Different foraging syndromes may have evolved in habitats which differ in patch structure. It is unlikely that morphological plasticity will enhance resource acquisition if patches are either much smaller or much larger than the distance between adjacent resource-acquiring structures (Sutherland and

Stillman, 1988). In addition, morphological responses may take place too slowly to allow effective exploitation of patches of high resource availability which only last for a short period of time. These considerations have led a number of authors to suggest that foraging for resource-rich patches is not a profitable behaviour in habitats with inherently low resource availability, in which resources become available in the form of ephemeral pulses (e.g. Grime *et al.*, 1986; Sibly and Grime, 1986; Hutchings, 1988; de Kroon and Schieving, 1990). Such habitats might be found, for example, in tundra communities (nutrient-poor) and in forest understoreys (light-poor). It is hypothesized that in such habitats more "conservative" methods have been selected for gaining resources, including resource-acquiring structures with a large total surface area placed on branches with low levels of morphological plasticity. In order to acquire the short-lived resource pulses, species in such habitats should be able to increase resource uptake and assimilation rapidly when resource levels increase—i.e. they should have high levels of physiological plasticity (Grime *et al.*, 1986; Campbell and Grime, 1989; Robinson, 1989). It is thus predicted that species of forest understoreys will possess a photosynthetic mechanism which is capable of effective carbon acquisition under a sunfleck regime, and that species from tundra will be highly plastic in nutrient uptake.

It is important to accept that several alternative foraging solutions for the acquisition of essential resources may be employed in a single habitat. For example, in relatively nutrient-rich habitats, some fast-growing species may dominate the vegetation ("space-consolidators" *sensu* de Kroon and Schieving, 1990) and maintain dominance for a considerable period of time. Selective placement of orthotropic shoots in high light patches may (de Kroon and Knops, 1990) or may not (Campbell *et al.*, 1991a) be important for the maintenance of the dominant position of such species. "Subordinate" species (*sensu* Grime, 1987), with a lower growth potential, may coexist in the same habitats by foraging efficiently in horizontal and/or vertical space (Campbell *et al.*, 1991a). If these subordinate species are clonal, they are likely to possess a guerilla growth form compared to a more phalanx growth form in clonal dominants (Lovell and Lovell, 1985). Such relatively guerilla species would be likely to exhibit a pattern of morphological plasticity characterized by a reduction of spacer length and an increase in branching intensity under more favourable conditions. This has been referred to as *the* foraging model in earlier publications (e.g. Sutherland and Stillman, 1988; de Kroon and Schieving, 1990; Oborny, 1991). Here we take a broader view and recognize other resource-acquiring syndromes as alternative examples of foraging behaviour. In particular, the foraging behaviours of orthotropic stems, plagiotropic stems and roots should be regarded as separate phenomena as they may have evolved independently in response to the particular types of environmental patchiness experienced by each of these types of organs.

B. Patterns

To what extent are these predictions borne out by the data reviewed in Sections III to VII? It has been shown in many species that branching indeed intensifies when resource levels increase. This is a very general response, observed in both shoots and roots and in response to a variety of resources. Branching is not only affected by local conditions; when resources are imported into one part of a plant from other parts, branching in the recipient part is usually also increased.

In orthotropic shoots and in roots, a reduction of spacer length under high resource availability is also a very general observation. Usually this is a local response which is relatively independent of the conditions experienced by other parts of the plant. Together with increased branching, the reduction in spacer length results in an increase in placement of resource-acquiring structures in favourable patches. The morphological responses of shoots have been found to be particularly sensitive to changes in the ratio of R/FR light, such as are caused by canopy shading. Stem analogues such as leaf sheaths respond just as vigorously as true stems. Lateral roots formed in nutrient-rich patches have relatively high growth rates, which increase local root surface area. While the extent of lateral root formation is highly plastic, the total length of the main root axis has been shown to be unresponsive to resource availability. Plasticity in root morphology is markedly reduced when roots are associated with mycorrhizal fungi. These fungi may adopt the foraging function of the roots. Fungi growing independently have also been shown to be able to search for, and converge efficiently upon favourable patches within the soil volume.

In contrast to both orthotropic stems and roots, the internode lengths of plagiotropic stems exhibit a variety of responses to resource availability. Under more favourable conditions, the formation of both shorter and longer internodes has been reported in different species; other species fail to show significant responses. For species which do shorten their internode lengths under high resource availability, the magnitude of the response seems to be much smaller than that shown by orthotropic shoots. As a result, plagiotropic stems are less capable of placing ramets selectively in favourable patches within a heterogeneous habitat. The total length of the axis of the plagiotropic shoot is again relatively independent of ambient conditions, even when internode lengths are plastic.

While the foraging patterns of orthotropic shoots and roots described above are qualitatively similar for many species, the magnitude of the responses differs widely; in some species the morphological responses to environmental quality are insignificant. Are these differences in foraging behaviour in accordance with the predictions which have been made for species from different habitats, as summarized above? There is some evidence that orthotropic shoots in shade-intolerant species are indeed more plastic than those of shade-tolerant species. It is less clear whether shade-tolerant species are better capable of utilizing sunflecks than shade-intolerant species. Sunfleck photosynthesis has been well studied, but few species have been compared to date.

The correlations between the levels of morphological and physiological plasticity of roots and the habitat of species are also weak. This may again be due in part to the fact that few comparative studies have yet been carried out. To date, it has not been conclusively shown that species from fertile soils are morphologically more plastic than species from infertile soils. The capacity to take up nutrients that are supplied in the form of ephemeral pulses can also be similar for species of both types of habitat. In general, the relative importance of morphological *versus* physiological plasticity for the exploitation of resource pulses of any duration has not yet been established. The capacity to maintain a large, viable root system under prolonged periods of nutrient depletion appears to be important for the efficient utilization of ephemeral nutrient pulses. This trait appears to be more characteristic of species from infertile habitats than of species from fertile habitats.

C. Evaluation

An appropriate null-model of foraging is that resource availability affects only the growth of the plant, without associated changes in modular construction occurring which would enhance the placement of resource-acquiring structures in localities with high resource availability. Increased growth implies the construction of larger branches, with greater branch length and diameter, and/or the production of a larger number of branches as a consequence of increased meristem activity. As growth proceeds, the probability of branching at a particular node in the plant's structure will usually increase.

The empirical patterns reviewed above show two almost universal responses which accord with the null-model: branching probability (meristem activity) at each node and branch diameter increase in response to increasing resource availability, although in some cases the changes are insignificant. However, the responses of branch (spacer) length convincingly falsify the null-hypothesis. Many examples exist of species which shorten their shoot and root spacer lengths under higher levels of resource availability. Stem analogues such as leaf sheaths respond as effectively as true stems. This observation is in support of a functional interpretation for the plasticity they exhibit. Changes in spacer length are local responses to ambient resource levels, and resources imported from other parts of the plant usually have little effect on the response. This also suggests that the responses are significant for foraging, rather than expressions of growth. As a result of shorter spacers and increased branching intensity, the placement of resource-acquiring structures is concentrated in more favourable patches of the environment, and, together with generally higher uptake rates, resource acquisition and growth may increase markedly. This set of responses is in accordance with the foraging hypothesis. Thus, while an example of enhanced growth, the response of branching may also be important for future resource acquisition.

Surprisingly, the responses of plagiotropic stems are usually qualitatively different from, and quantitatively smaller than, those of orthotropic stems. Qualitatively different responses to light availability are unexpected, given the homology of these organs (Sachs, 1988). This is especially true for above-ground stolons. However, subterranean plagiotropic stems (rhizomes) are architecturally less similar to orthotropic stems and phylogenetically more ancient (Mogie and Hutchings, 1990). Thus, they may not exhibit foraging responses because such responses were probably not ancestral traits. The primary function of rhizomes may be storage. If this is the case, the longer rhizomes which are formed under higher resource availability in some species should be interpreted as expressions of resource accumulation and growth.

A corollary to the quantitatively small responses of plagiotropic spacer lengths is that the habitat is continuously searched. When favourable patches are encountered, the foraging responses of the shoots and roots of individual ramets enable efficient exploitation of the resources to take place without compromising the rate of exploration of horizontal space. It is worth recalling (Section V.A) that the length of main root axes has also been shown to be unresponsive to resource availability, enabling the root system to search the soil volume continuously. Orthotropic shoots do not exhibit this behaviour but always shorten under higher levels of photon flux density. Possession of an elongation response in orthotropic shoots can be profitable because the growth of these shoots is nearly always directed towards the high light zone in the top of the canopy. Roots and plagiotropic stems experience a patch structure which is less predictable and this may warrant the continuous exploration of new microhabitats for resources.

The data collected so far do not unambiguously support the premise that species from different habitats possess markedly different patterns of morphological and physiological plasticity. Species differ in the extent to which they are morphologically and physiologically plastic, but correlations with habitat type are at best incomplete. A notable exception is the extension response to light availability in orthotropic shoots. This is generally far greater in shade-intolerant than shade-tolerant species, which suggests that vigorous stem height extension has been selected in shade-intolerant species as a response to above-ground competition for light. For the acquisition of ephemeral resource pulses in resource-poor habitats, the ability to survive periods of resource depletion appears to be at least as important as the possession of higher levels of physiological plasticity. This ability is enhanced by economic use of resources and slow growth. These characteristics are typical for species from resource-poor habitats (Berendse and Aerts, 1987; Lambers and Poorter, 1992; Aerts and van der Peijl, 1993).

D. Unsolved Questions

The juxtaposition of hypotheses and patterns draws attention to significant gaps in our knowledge about the foraging behaviour of plants. Here we identify some of the gaps in order to suggest topics for future research.

1. Generality of Responses

In order to reveal general trends in foraging behaviour, data are needed from a large number of species. Because comprehensive sets of data are lacking, it is as yet unclear whether there is a tendency for species from habitats which contrast in resource availability to differ in the levels of morphological and physiological plasticity which they possess. Comparative studies in which traits are screened in a large number of species (see for example Grime *et al.*, 1981; Poorter *et al.*, 1990; Westoby *et al.*, 1990) are advocated as a remedy. There is a special need for between-species comparison of those plastic characteristics which have only been examined in a few species, but for which the regulation mechanism has been well elucidated. One such example involves the physiology of light fleck photosynthesis, which has been extensively studied, but about which information has been collected from a very limited number of species. Another subject about which much is known is the mechanism underlying the etiolation of stems in response to a change in light quality. In most experiments in which morphological plasticity has been investigated in species with plagiotropic stems, however, consideration has only been given to the analysis of responses to variation in light *quantity*, rather than quality. Rectification of this situation would be informative.

2. Patch Structure, Patch Quality and the Profitability of Different Types of Behaviour

In recent years an increasing number of papers has been published describing the patch structure of different habitats. The importance of these studies for the interpretation of foraging responses cannot be emphasized too strongly. The profitability of any level of morphological plasticity will depend on the spatial and temporal variability in resource supply within the habitat (Harper, 1985; Sutherland and Stillman, 1988), but virtually nothing is known about the nature of this relationship. Many studies on morphological plasticity, including some of our own (e.g. Slade and Hutchings, 1987a,b; de Kroon and Knops, 1990) implicitly assume that the grain of environmental heterogeneity will match average spacer length so that plasticity will lead to an advantage to the plant in terms of its resource acquisition. However, this premise is rarely put to the test. In combination with ongoing efforts to quantify patch structure, we believe that studies of plasticity should increasingly be directed towards quantification of the advantages of the particular behaviours which are displayed by species in given environmental settings, compared with other possible behaviours.

3. Comparative Plasticity of Different Types of Spacers

One question which emerges from the concept of foraging as a general phenomenon, is whether different types of spacers employ similar solutions when contending with a given problem of environmental heterogeneity. Few studies have compared the foraging characteristics of spacers such as orthotropic stems, plagiotropic stems, stem analogues (such as petioles and leaf sheaths), and roots. It can be hypothesized that the degree of morphological plasticity shown by a spacer is attuned to the pattern of resource heterogeneity which it encounters. Alternatively, it has been suggested that high levels of morphological plasticity are expressions of strong competitive ability in a species, and hence that a positive correlation is expected between the levels of plasticity exhibited by roots and shoots (Campbell *et al.*, 1991a,b). Tests of such hypotheses call for studies in which levels of plasticity are compared between organs in a variety of environmental conditions, and in which the overall benefits of a given behaviour are measured in terms of competitive ability and resource acquisition. It should also be accepted that the generally low levels of plasticity observed in plagiotropic stems can perhaps only be understood if the plasticity of the roots and shoots of the same species is also considered. However, the relative benefits conferred by different degrees of plasticity in each of these organs have never been assessed for any plant species.

4. Morphological versus *Physiological Plasticity*

An acute unsolved problem is determination of the relative importance of morphological *versus* physiological plasticity in a given environmental setting. One way of tackling this problem empirically is to subject closely related species (or genotypes or varieties of single species) which differ in these modes of plasticity to environments with a specified patch structure, and to measure their rates of acquisition of essential resources. Studies of this type on phosphate acquisition with species of bunchgrasses (Caldwell *et al.*, 1991a,b); Van Auken *et al.*, 1992) have provided evidence which suggests that physiological plasticity may be more important for resource acquisition in patchy environments than previously thought. Further studies should be carried out on this topic. In addition there is a need for similar experiments in which patch duration is varied. Other suitable combinations of species or subspecies for comparison can easily be identified (for published examples see, e.g., Poorter and Lambers, 1986; Callaway, 1990; Tinoco-Ojanguren and Pearcy, 1992). Ultimately, simulation studies will be a necessary tool to compare the merits of morphological *versus* physiological plasticity (Caldwell *et al.*, 1992; see Section X).

5. *Foraging Intensity and Whole-plant Growth*

Are the patterns of shoot and root foraging modified in similar ways if the growth of the whole plant is resource limited? It has been shown that both root branching and root elongation increase more vigorously in response to higher local levels of nutrient availability if the nutrient demand of the whole plant is higher. We can also enquire whether shoot branching and leaf production will increase more markedly in high light patches if the growth of the plant is more carbon limited than when it is not. Such responses would be expected because higher levels of branching under the same regimes of photosynthetically active radiation may increase assimilate production (see Novoplansky *et al.*, 1990b), but to our knowledge no experiments have been carried out to examine this phenomenon.

6. *Foraging and Resource Integration in Clonal Plants*

If part of an integrated clonal plant growing under low resource levels imports resources from another part of the clone growing under more favourable conditions, one would expect that morphological responses to local resource scarcity will be damped as a result of the elevation of internal resource concentrations. Surprisingly, it appears that this is not always the case. Instead, integration may even intensify the morphological responses to local growing conditions (see Alpert, 1991; Evans, 1992). The physiological mechanism behind this reaction and the functional significance of integration for local foraging responses deserve further study. One hypothesis to explain this result is that augmentation of the local response could stimulate a behaviour which would promote escape from locally unfavourable conditions. Integration could thus increase foraging efficiency in a patchy habitat, in contrast to suggestions made by de Kroon and Schieving (1990). The importance of local foraging and integration for resource acquisition may markedly increase if habitat patches are characterized not by some level of favourability, but instead by an adequate supply of some resources and an inadequate supply of others. The consequences of plasticity and integration in such a multiple-resource habitat patch structure are only now beginning to be considered.

7. *Mechanisms and Constraints*

Some of the mechanisms underlying the foraging responses of plants to variable environmental conditions are still elusive. For example, there is still no clear understanding of the way in which environmental conditions affect apical dominance through changes in the levels of, or the sensitivity to, plant growth substances. The importance of such regulation mechanisms underlying plasticity should be emphasized. The developmental and physiological traits behind the responses that we observe are the traits which are heritable. Some of these traits may be readily modified by natural selection while others may be embedded in a developmental program which constrains their evolution (Sachs, 1988). Indeed, some of the similarities observed in morphological plasticity between species may be due to phylogenetic constraints (de Kroon and van Groenendael, 1990; Fitter and Stickland, 1991), while other morphological characteristics may vary widely within a genus (Mogie and Hutchings, 1990). Another constraint acting on the evolution of plasticity may be a (physiological or genetic) trade-off between morphological and physiological plasticity, causing species with marked morphological *and* physiological plasticity to be rare, as suggested by Fitter and Stickland (1991). Ultimately, information on traits underlying plasticity, and on the inheritance of these traits, will be indispensable for an understanding of the ecological and evolutionary significance of phenotypic plasticity.

X. TOWARDS A FORAGING RESEARCH PROGRAMME

This review has presented information about plasticity in the modular construction of plants, and the consequences of this plasticity for the placement of resource-acquiring structures within a heterogeneous environment. Our ultimate goal is to understand the advantages of different resource-acquiring syndromes and their ecological and evolutionary consequences. An investigation of morphological plasticity will be only one of the elements, albeit an essential one, in a research programme which is directed towards the goal of evaluating foraging behaviour. A complete and accurate evaluation of foraging behaviour requires an assessment of its economics, i.e. a quantification of its costs and benefits. Such an analysis must be based on the premise that the behaviour which results in the highest net resource extraction from the environment will have a selective advantage. Here we outline the requirements for an analysis of the costs and benefits of foraging in plants, as a perspective for future research.

A. Cost–Benefit Analysis

In accordance with foraging models (Stephens and Krebs, 1986) and current views about the costs of plant structures (Bloom *et al.*, 1985; Chapin, 1989), we define the costs of a certain behaviour as the long-term resource investment in spacers at the level of the whole plant. The benefits are defined as the long-term resource extraction. An appropriate unit of measurement is the amount of resources invested or acquired per unit of plant biomass and per unit of time. Following Hunt *et al.* (1990), the efficiency of foraging can be expressed as the amount of resources captured as a proportion of the amount of resources that the environment supplies. The growth that the plant can achieve will depend, in turn, on the efficiency of resource utilization, i.e. the rate of biomass production per unit of resource captured. Note that it is not the strategy with the highest efficiency, but the strategy with the highest resource gain per unit of time which is most advantageous in a given environmental setting (cf. Stephens and Krebs, 1986).

Figure 10 illustrates the different components of a cost–benefit analysis of foraging, and their interrelationships. The costs of investment in plant structures can be divided between the costs of construction and costs of maintenance. There will also be *negative* costs associated with the resorption of resources from dying plant parts. Such costs are the subject of an extensive body of literature (e.g. Chapin, 1989; Jonasson, 1989; Carlsson and Callaghan, 1990; Pugnaire and Chapin, 1992). Costs of maintenance may be significant for carbon due to respiration, but low for mineral nutrients, while a large proportion of the invested nutrients but hardly any carbon may be recovered when plant structures senesce (Chapin, 1989). These processes have been extensively documented for leaves but much less so for spacers such as orthotropic and plagiotropic stems. A notable exception is provided by work on tundra species in which resorption of nutrients from senescing plagiotropic spacers was shown to be between 50 and 90% (Callaghan, 1980; Headley *et al.*, 1985; Carlsson and Callaghan, 1990). Investment costs of spacers in terms of the allocation of resources per plant per year may thus be relatively small, especially for nutrients. Although methods for calculating such costs are readily available, to our knowledge no such cost analyses have been carried out to date.

An important, but largely unexplored element in the cost–benefit analysis of foraging, is the relationship between morphological plasticity and investment costs. Resource investment in spacers is likely to increase with spacer length, but this relationship will not be proportional if longer spacers are also thinner, as for shoots growing under shade (Hutchings and Mogie, 1990). For example, when growing under low photon flux density, *Glechoma hederacea* produces stolon internodes which are 50% longer but which have a 40% lower weight than the internodes of clones growing at high photon flux density (Slade and Hutchings, 1987b). Consequently, under unfavourable light conditions longer stems may be produced with little if any costs in terms of reduced biomass allocation to leaves and roots. An illustration of this has recently been seen in *Amaranthus quitensis* (Ballaré *et al.*, 1991b).

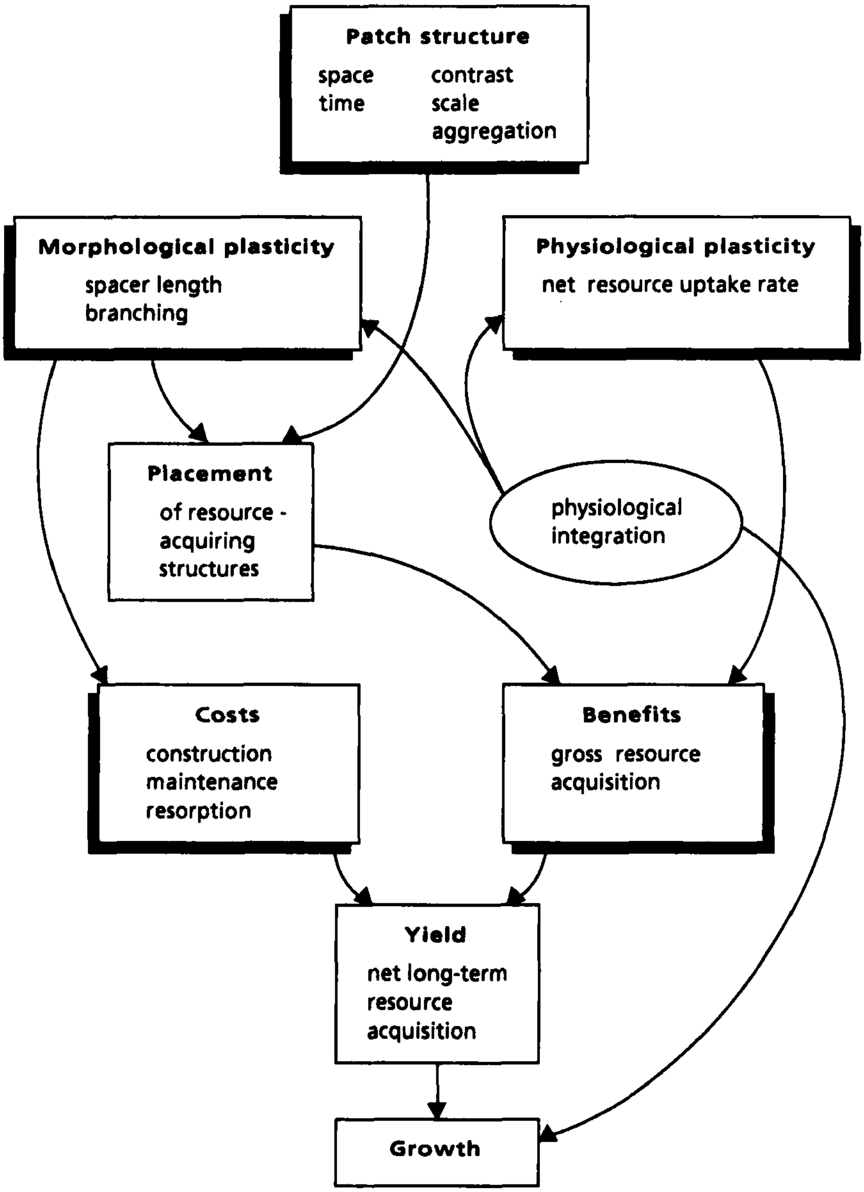


Fig. 10. A diagram of the components of a plant foraging research programme, and the interrelationships between these components. Central elements are the levels of physiological and morphological plasticity and how they influence the costs and benefits of foraging, mediated by the patch structure of the habitat.

If the production of longer spacers is combined with reduced branching intensity, the relationship between morphological plasticity and resource investment becomes more complex. De Kroon and Schieving (1991) formulated a simplified branching model of a clonal plant and calculated the allocation to spacers as a function of resource availability, based on plastic changes in the length and specific weight of spacers and the weight of ramets. Simulations showed that opposing responses in branching intensity and spacer length may compensate for each other in such a way that resource investment in spacers was equal under both low and high resource availability. Surprisingly, this compensation appeared to be incomplete when intermediate levels of resources were available, so that resource investment in spacers was predicted to be larger under these conditions. One virtue of formalizing the relationship between plasticity and investment is that it highlights factors which are important determinants of the relationship, but which are easily overlooked. The model of de Kroon and Schieving (1991; and 1990 using a preliminary version of the model) suggests that the developmental time of spacers *versus* ramets—i.e. the time each of these structures needs to reach its maximum weight—may be critical for the amount of resources allocated to spacers. Such developmental times are only now beginning to be regarded as important attributes for ecological study (e.g. the plastochron index; Birch and Hutchings, 1992; Dong, 1993).

As emphasized above, the patch structure of the habitat is a critical factor governing the benefit gained from morphological plasticity. The pattern of habitat heterogeneity, together with the degree of morphological plasticity which a species exhibits, will determine the extent to which resource-acquiring structures will be placed in the more resource-rich patches of the environment. Ultimately, both morphological and physiological plasticity will contribute to the amount of resources captured by a plant (Fig. 10). The costs of physiological plasticity (the energetic costs of resource uptake and assimilation), and of resource transport, also have to be included in any cost–benefit analysis, although they are not shown separately in Fig. 10 for the sake of simplicity. Physiological integration may modify the magnitude of both the morphological and physiological responses and hence will change the quantity of resource accumulated. By enabling translocation of resources from ramets with low growth rate to ramets with high growth rate, integration could also increase the resource utilization efficiency and growth of a clonal plant (Caraco and Kelly, 1991; see Salzman and Parker, 1985; Slade and Hutchings, 1987d).

B. Foraging Models

Significant progress in plant foraging research will be possible if the different elements depicted in Fig. 10, and their relationships, are modelled and interrelated. The development of such foraging models may already be within reach because most of the components involved have been formalized.

The patch structure of a habitat can be characterized by the contrast in quality between patches (the relative differences in their resource supply) as well as by their scale and distribution in space and time (Addicot *et al.*, 1987; Kotliar and Wiens, 1990). A measure of environmental predictability could also be usefully devised to allow comparisons between habitats (Oborny, 1994). For clonal plants, there is a variety of models which simulate morphological plasticity and the placement of ramets in patchy environments (Ford, 1987; Sutherland and Stillman, 1988, 1990; Oborny, 1994; see also Rubin, 1987), while other spatially explicit models (Bell, 1986; Callaghan *et al.*, 1990; Cain *et al.*, 1991; Klimes, 1992; Cain, 1994) could easily be adapted for this use. There are as yet fewer models of this type for orthotropic shoots and roots (Aono and Kunii, 1984; Bell, 1986; Fitter, 1987). From a knowledge of the patch structure of the habitat and the amount of morphological plasticity available in a species, spatial models will enable prediction of the local conditions that resource-acquiring structures will experience. Models of nutrient uptake (Nye and Tinker, 1977; Barber, 1984; Robinson, 1989; Caldwell *et al.*, 1992) or of photosynthesis (Gross *et al.*, 1991) will then allow calculation of the quantity of resources acquired by the species (i.e. the "benefits" in Fig. 10), taking into account the level of physiological plasticity that the species exhibits. Lastly, investment costs of spacers may be calculated based on estimates of the amount of resources involved in construction, maintenance and resorption (see Chapin, 1989). By using allocation models such as that of de Kroon and Schieving (1991), the effects of morphological plasticity on these costs can also be incorporated.

It is beyond the scope of this review to dwell on the goals of foraging models. Here we confine ourselves to identifying two complementary aims. First, using the scheme of Fig. 10, theoretical models can be constructed to generate hypotheses about probable foraging behaviour in a habitat with a generalized patch structure. Those constraints on the possibilities for foraging behaviour, which are dictated by physiological and genetic regulation mechanisms, should be taken into account in such modelling. Secondly, models may be formulated in which each of the elements of the foraging process is calibrated on the basis of empirical data. With both of these approaches, each of the components is interrelated and the net benefits calculated in terms of net long-term resource extraction. The relative importance of, for instance, morphological *versus* physiological plasticity could be assessed by means of sensitivity analyses, and foraging efficiencies could be computed. Specific foraging syndromes could be contrasted with null-models in which plants place their resource-acquiring structures at random within the habitat, or according to fixed growth rules. It should be possible to identify the environmental parameters with the strongest impact on foraging behaviour. Ultimately, modelling approaches will prove to be imperative in solving the questions raised in the previous section.

We believe that plant and animal foraging can be fruitfully related by comparing the economics of behaviour in relation to the patch structure of the habitat. As a consequence of such comparison, the use of the term foraging in plant ecology will surpass the level of a metaphor (see Oborny, 1991). At the same time, despite the same underlying economic principles, some animal foraging models (such as the Marginal Value Theorem) will only be applicable to plants after considerable adjustment. Many of the assumptions of these models, such as decisions being taken prior to resource uptake, a finite amount of resources per patch (and hence the exhaustion of the patch through the activities of a foraging organism), the discrete nature of patches and resources (prey), and the separation in time of search and exploitation (Stephens and Krebs, 1986), may apply directly to plants only in exceptional cases (Kelly, 1990). It will be a challenge to formulate such adjustments to generate models which are applicable to both plants and animals, and to seek a unified foraging theory to encompass both.

> Elsewhere immense research into the nature, habits and constitution of the triffid went on. Earnest experimenters set out to determine in the interests of science how far and for how long it could walk; whether it could be said to have a front, or could it march in any direction with equal clumsiness; what proportion of its time it must spend with its roots in the ground; what reactions it showed to the presence of various chemicals in the soil; and a vast quantity of other questions, both useful and useless.
>
> (from John Wyndham, *The Day of the Triffids*, 1951)

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